EXPLAINING PATTERNS OF DOMINANCE IN OLD-FIELD COMMUNITIES: TRADE-OFFS, FEEDBACKS, MUTUALISMS AND ENEMIES

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Submitted to the Graduate Faculty of

the Kenneth P. Dietrich School of

Arts and Sciences in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy in Ecology and Evolution

University of Pittsburgh

2013

UNIVERSITY OF PITTSBURGH

DIETRICH SCHOOL OF ARTS AND SCIENCES

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Although one of the oldest observations within ecology is that within communities there are few common species with many uncommon and rare species, the mechanisms that shape this relationship remain elusive. The primary explanations for repeated dominance in plant communities lie in competition theory, which predicts specific allocation to resource acquisition, low resource tolerance, colonization, and herbivore tolerance and resistance. Alternatively, soil community feedback theory predicts positive plant-soil feedbacks to alter competitive dynamics and lead to dominance. Finally, specific mutualistic clades of the soil community, such as mycorrhizal fungi, may increase resource acquisition or herbivore tolerance, thus promoting positive feedback. To address these mechanisms that contribute to relative abundance and dominance, I used a light limited, old-field model system. Although these systems are relatively diverse, there is a striking pattern of repeated dominance by *Solidago canadensis*. By using a series of greenhouse and manipulative, long-term *in situ* experiments, I found no "smoking gun" mechanism to explain the dominance of *So. canadensis*, but rather an entire suite of processes that likely contribute to relative abundance and the maintenance of diversity. I found no evidence of life history trade-offs across old-field species, with *S. canadensis* consistently violating long-standing theory by being the best light competitor, most shade tolerant, most herbivore resistant, most herbivore tolerant, and among the fastest growing species. Looking belowground, I found that old-field plant species, even coexisting congeneric species, culture significantly different soil microbial communities, which altered plant performance, changed the intensity of interspecific competition and reversed whether plant species were limited by conspecifics or heterospecifics. Although this mosaic of shifting competitive abilities due to soil feedbacks is predicted to maintain diversity, the ability of *S. canadensis* to grow well in its own and competitor soil communities may foster *S. canadensis* invasion and subsequent defense of territory. Finally, mycorrhizal fungi increased herbivore tolerance across old-field species, while having little or negative effects on plants in the absence of herbivory. This process may promote diversity within old-fields, but offers insight into how *So. canadensis* maintain dominance in the face of dozens of specialist herbivores.

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INTRODUCTION

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?" Darwin (1859)

One of the oldest observations within the ecological literature is that within almost any community there are a few common species with the remainder of the species pool generally uncommon to rare. This spurned a tremendous exploration of species area distributions (SAD) in the 20th century, from Raunkiaer (1909), Fisher et al (1943), Preston (1948) and MacArthur (1960) to more recent descriptions of the relative abundance of tropical tree species on Barro Colorado Island in Panama (Hubbel 1997). Of the dozens of species area distribution models, the vast majority focused on explaining the hollow curve of species abundance – such that SAD's were dubbed "the science of scarcity" (Soule 1986). This has tremendous merit, of course – explanations for these patterns are likely to inform the maintenance of diversity and conservation of rare species. However, here, I would like to reverse the question: what allows a very limited number of species to compose a majority of the community? What processes are likely to contribute to dominance?

The primary explanations for repeated dominance in plant communities lie in competition theory. Conventional wisdom suggests that these repeated patterns occur because

these species are the superior competitor, though surprisingly there have been few studies that have verified this experimentally. Indeed, a striking circularity exists with regard to dominant plant species and their competitive ability, specifically dominant species are the superior competitors and the superior competitors are the dominant species (Gurevitch et al. 2006). There are, of course, alternative explanations for why any plant species becomes dominant. These species may indeed be the best competitors by rapidly drawing down resources (Tilman 1977, 1980, 1982) or by surviving resource suppression (Goldberg and Werner 1983, Goldberg 1990, Goldberg and Fleetwood 1987, Goldberg and Landa 1991). Alternatively, these dominant species may enjoy positive soil community feedbacks (Bever 2003), strongly resist or tolerate their enemies (Grover 1997), colonize open space quickly (Levins and Culver 1971), or they may form better relationships with their putative mutualists (Bever et al 2002).

To address the mechanisms that contribute to relative abundance and dominance, I used a light limited, old-field model system (Carson and Pickett 1990, Bazzaz 1996, Carson and Root 2000). Old fields are common throughout the northeast and mid-Atlantic United States as a byproduct of agriculture abandonment. The old-field overstory is generally comprised of goldenrod and aster species (Asteraceae) (Bazzaz 1996, Carson and Root 2000). Although these systems are relatively diverse, there is a striking pattern of repeated dominance by *Solidago canadensis* in the vast majority of these fields (Bazzaz 1996, Carson and Root 2000). While old fields have been used extensively for ecological study (e.g., Gurevitch et al. 1990, Bazzaz 1996, Root 1996, Carson and Root 1999, Kosola and Gross 1999, Stevens and Carson 1999a, Stevens and Carson 1999b, Carson and Root 2000, Long et al. 2003, Stevens et al. 2004, Banta et al 2008), the mechanism(s) behind *S. canadensis*' competitive dominance remains unknown.

Here, I examine a number of theoretical frameworks to understand patterns of relative abundance within old-fields well as search for explanations for the consistent and repeated dominance of *Solidago canadensis*.

1.1 TRAIT AND TRADE-OFFS

Plant traits and tradeoffs lie at the core of species coexistence theory, and they are predicted to be the key drivers of plant community dynamics and resulting structure. Tilman (1988, 1990) has argued that species-specific allocation tradeoffs should correlate with hierarchies of competitive ability, relative abundance, and coexistence in plant communities. We examined 6 classic and well established life history trade-off predicted to maintain diversity within communities, but also inform patterns of relative abundance: 1. *Competition-Colonization* (e.g., Levins and Culver 1971); 2. *Competition-Herbivore Resistance* (e.g., Tilman 1990a); 3. *Colonization-herbivore resistance* (e.g., Strauss et al. 2002); 4. *Growth rate-herbivore resistance* (e.g., Coley et al. 1985); 5. *Herbivore resistance-herbivore tolerance* (e.g., Mauricio 2000); 6. *Competition mechanisms: resource tolerance-resource reduction* (e.g., Miller and Werner 1987). Old-fields in the United States and southeastern Canada have light-limited understories, with moderate to high soil resource availabilities (Bazzaz 1996); thus, we hypothesized that species that allocate relatively more to growth, light attenuation, and herbivore tolerance should be more abundant, relative to species allocating more to colonization and herbivore resistance (Coley et al. 1985, Tilman 1988, 1990a). To test these hypotheses and relationships, I examined the plant traits of 9 old-field plant species grown in long-term monocultures, factorially manipulating insect and mammalian herbivores.

1.2 SOIL COMMUNITY FEEDBACKS

Understanding the extent and strength of plant-soil community dynamics is critical to identify mechanisms that determine plant competitive outcomes, relative abundance, and coexistence (Bever 2003). Overall, little is known about belowground soil communities and their general roles in driving plant community dynamics. This is certainly understandable given the staggering diversity in belowground communities; a gram of soil can harbor over 5000 species of microorganisms (Torsvik et al. 1994). To address the potential impact of these radically diverse communities on plant performance and community dynamics, we tested the 3 tenets of the Soil Community Feedback model. Specifically: *1. The Host Specificity hypothesis***:** plant species "culture" their own specific microbial and microzoan community within their rhizosphere**.** *2. The Plant Feedback hypothesis:* the development of species-specific microbiotic communities subsequently influences the performance of con- and heterospecific plants (Bever et al. 1997). *3. Feedbacks and Competitive Hierarchy hypothesis:* the development of contrasting soil communities alters plant performance sufficiently to change the competitive hierarchy and thus population dynamics of coexisting species (Bever 2003). Local feedback interactions potentially scale up to drive patterns of relative abundance; specifically, positive feedbacks are predicted to increase plant abundance. We therefore hypothesized that more positive feedbacks, relative to other species, may help *So. canadensis* dominate these communities. To test these hypotheses, we used a comprehensive combination of genetic tools, soil community cultivation, and a series of intra- and inter-specific competition experiments.

1.3 MYCORRHIZAL DEPENDENCY AND KEYSTONE PREDATION

All species exist within complex trophic webs characterized by cascading and indirect effects that potentially mediate the structure of communities and patterns of dominance (e.g., Wootton 1994). Here, I focus on two specific processes that likely structure many plant communities: keystone predation and mycorrhizal dependency. Insect herbivores may function as classic keystone predators (*sensu* Paine 1966) by reducing the performance and abundance of the competitive dominant and thereby promoting diversity. Similarly, variation in mycorrhizal dependency across species can enhance resource availability to subordinate species, promoting coexistence and maintaining diversity (Gange 1993, Karanika et al. 2008). However, some mycorrhizal dependent plants become dominant *because* of the their mycorrhizal associations (Hartnett and Wilson 1999). I note that this mutualism can be costly: plants allocate 4-20% of the plant's total carbon budget toward supporting their symbiotic fungi (Bago et al. 2000, Douds et al. 2000, Graham 2000). In return, arbuscular mycorrhizal fungi (AMF) increase water and nutrient transfer from the soil (Allen et al. 1981, Smith and Read 1997), potentially delivering 80% of a plant's phosphorus budget, and up to 25% of the nitrogen requirement (Marshner and Dell 1994).

Here I ask how mycorrhizal relationships change with realistic biotic complexity (herbivore stress). These associations are known to be species- and environment specific (van der Heijden et al. 1998a, Wilson and Hartnett 1998, Vogelsang et al. 2006), and the nature of the relationship can span from obligately mutualistic to potentially parasitic (Johnson et al. 1997, Wilson and Hartnett 1998, Johnson et al. 2003, Klironomos 2003, Jones and Smith 2004). However, due to the consistent dominance of *Solidago canadensis*, I predicted that AMF are likely beneficial to goldenrods or at least beneficial under stress. Furthermore, I predicted that

associations with mycorrhizal fungi should be most beneficial in the presence of herbivores, and that the degree of benefit should increase with relative abundance. To test these predictions, I examined the plant performance and competitive ability of 7 old-field plant species grown in long-term monocultures, factorially manipulating insect herbivores and mycorrhizal fungi.

1.4 "THE SMOKING GUN"

I have taken a varied approach to understanding patterns of relative abundance in old-field systems in the hope of identifying a single or combination of traits or processes that explain the consistent dominance of *Solidago canadensis.* These approaches range from completely black box (Soil Community Feedback) to specific manipulations of different trophic levels. I used 7-9 plant species in long-term, *in situ* monocultures; a species pool that comprises more than 60% of the local community by density (Pendergast, unpublished data). I therefore expect that if we uncover the primary mechanisms that drive old-field community structure with this suite of species, those mechanisms are likely critically operating in tens of thousands of old fields throughout midwestern and northeastern North America.

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2.0 EVIDENCE FOR A HUTCHINSONIAN DEMON: LACK OF LIFE-HISTORY TRADEOFFS PREDICTS DOMINANCE

2.1 INTRODUCTION

Much ecological theory has focused on the inherent constraints and life-history tradeoffs among species to explain coexistence (Gause 1932, Hardin 1960, Levin 1970, Tilman 1982, Chesson 2000). This cornerstone of ecology is based on the premise that all organisms have limited resources to allocate to contrasting life history demands, and that traits alone and in combination are constrained by genetics, phylogeny, physiology, and/or resource availability (Tilman 1988, 1990a, Stearns 1992, Cox and Calsbeek 2010, Goodwillie et al. 2010). Character displacement that occurs among species (e.g., resource specialization) is predicted to increase the opportunity for coexistence via niche differentiation (Tilman 1994a, Leibold 1998, Tessier et al. 2000, Chase et al. 2001, Cadotte 2007b). While there are numerous predicted tradeoffs for plants (reviewed in Tilman 1990a, Crawley 1997, Kneitel and Chase 2004), the evidence for the existence of tradeoffs in the literature is definitely mixed (e.g., Yu and Wilson 2001, Calcagno et al. 2006, Ridenour et al. 2008, Mooney et al. 2010). Nonetheless, the vast majority of our theory remains dependent on trait differences (but see Hubbell 1997), and explicitly predict that these

tradeoffs must operate within communities at both local and regional scales. The specific critical tradeoffs that allow coexistence are likely to change both temporally and spatially, as well as across communities, resource availabilities, and trophic structure (Grime 1977, Tilman and Kareiva 1997, McPeek 1998, Ritchie et al. 1998, Suding et al. 2003). Most studies only examine a single tradeoff, even though multiple tradeoffs are likely to operate simultaneously within a community (but see Tilman 1990a, Suding et al. 2003).

Not only are traits and tradeoffs at the core of species coexistence, they are predicted to be the key drivers of plant community dynamics and resulting structure. Tilman (1988, 1990) has argued that species-specific allocation tradeoffs should correlate with hierarchies of competitive ability, relative abundance, and coexistence in plant communities. Contrasting plant communities filter for particular traits or suites of traits (e.g., Weiher and Keddy 1999) and both functional and life history traits have been successfully used to predict patterns of relative abundance among species within a community (Wedin and Tilman 1993, Vojtech et al. 2007, Cornwell and Ackerly 2010). For example, the classic competition-colonization tradeoff predicts eventual dominance by the best competitors in the absence of disturbance while better colonizers coexist by quickly acquiring unoccupied territory (Levins and Culver 1971, Horn and Mac Arthur 1972, Hastings 1980, Tilman 1993, 1994b, Chase et al. 2001, Levine and Rees 2002, Kisdi and Geritz 2003, Cadotte 2007a).

In light limited systems, increased allocation to shoots should increase competitive ability by increasing light interception (Tilman 1988, Bazzaz 1990, Schmid and Bazzaz 1990, 1992, Bazzaz 1996, Vojtech et al. 2007). In communities of long-lived herbaceous species (e.g., grasslands), clonal herbaceous plants may face a very simple allocation decision: allocation to vertical shoots to capture more light vs. allocation to horizontal shoots (vegetative spread) to

capture new territory (Bazzaz 1990, de Kroon and Hutchings 1995, Bazzaz 1996, Ye and Dong 2006). Consequently, dominant species in light limited habitats should have traits that maximize their ability to acquire light and form dense clonal stands. Alternatively, clonal species that capture territory by rapidly spreading into new habitats with longer stolons or rhizomes cannot form dense clones capable of casting deep shade. If subordinate species are inferior competitors, they may coexist with superior competitors by rapidly colonizing open sites, thereby avoiding competitive exclusion as long as open sites remain available (Tilman 1994b, Pacala et al. 1996, Hartley 1999, Calcagno et al. 2006, Cadotte 2007a). This framework can be extended to other crucial allocation and life history tradeoffs to similarly predict relative abundance, dominance, and coexistence across temporal and spatial scales.

Critical life history tradeoffs

Here, we focus on 6 life-history allocation tradeoffs commonly predicted to occur within and across communities:

1. Competition-Colonization: The classic *r-K* continuum; allocation to investments in growth and resource acquisition structures represents resources that could have increased reproductive output (Levins and Culver 1971, Horn and Mac Arthur 1972, Hastings 1980, Tilman 1993, 1994b, Chase et al. 2001, Levine and Rees 2002, Kisdi and Geritz 2003, Cadotte 2007a).

2. Competition-Herbivore Resistance: Allocation to defensive traits, especially where herbivore damage is minimal, represents resources that could have been allocated to above- or below-ground resource acquisition structures (e.g., Gulmon and Mooney 1986, Tilman 1990a,

Haag et al. 2004, Kurashige and Agrawal 2005, Viola et al. 2010, Beaton et al. 2011). We define herbivore resistance operationally as the inverse of the amount of feeding damage suffered *in situ* after plant monocultures reach equilibrium (Simms and Rausher 1987, Mauricio 2000, Wise 2007).

3. Colonization-herbivore resistance: Allocation to defensive traits, especially where herbivore damage is minimal, represents resources that could have increased reproductive output and population growth rate (e.g., Bazzaz et al. 1987, Strauss et al. 2002, Hare and Smith II 2005, Hakes and Cronin 2011).

4. Growth rate-herbivore resistance: Resource limitation and the high costs of herbivory result in slow growth and high allocation to herbivore resistance traits, while greater resource availability is predicted to favor faster growing, poorly defended species (e.g., Coley et al. 1985, Coley 1986, Bazzaz et al. 1987, Herms and Mattson 1992, Hartley and Jones 1997, Endara and Coley 2011). While related to competition-herbivore resistance tradeoff, this hypothesis is based on predictions of allocations to growth versus defense along resource gradients and makes no predictions on competitive ability.

5. Herbivore resistance-herbivore tolerance: Allocation to costly morphological and chemical traits or both that confer herbivore resistance is predicted to decrease the physiological ability to compensate for damage and thereby tolerate herbivory. We define herbivore tolerance as ability to compensate or maintain biomass in the presence of herbivores. It is important to note that allocation to multiple distinct mechanisms of herbivore mitigation is functionally

redundant and wasteful if they are a response to similar suites of enemies (Van der Meijden et al. 1988, Fineblum and Rausher 1995, Tiffin and Rausher 1999, Chase et al. 2000, Mauricio 2000).

6. Competition mechanisms: resource tolerance-resource reduction: Allocation to morphology and physiology that allows rapid resource acquisition is predicted to decrease survivorship as environments become stressful and resources scarce. While the primary mechanisms of competition have been hotly debated (Grime 1977, Goldberg 1990, Tilman 1990b, 1997, Howard and Goldberg 2001, Aarssen and Keogh 2002, Craine et al. 2005, Tilman 2007), here we hone in on a poorly resolved tradeoff between competitive effect (the ability to draw down limiting resources, .e.g. cast shade) and competitive response (the ability to survive resource suppression, e.g., shade tolerance). We note that this is not a classic tradeoff *per se*, but at the very least these traits are predicted not to be positively correlated (Howard and Goldberg 2001) and can be negatively correlated (Miller and Werner 1987, Hager 2004).

We use this framework to gain insight into a long-standing pattern in ecology – the dominance of a group of long-lived perennials (goldenrods, primarily *Solidago canadensis*) over dozens of other coexisting species for three or more decades after agricultural abandonment throughout large portions of the northeastern and mid-western United States and southern Canada (Carson and Pickett 1990, Bazzaz 1996, Carson and Root 2000, Banta et al. 2008). Bazzaz (1996) concluded that *Solidago* achieved near monodominance by slow, dense clonal expansion ('phalanx' clonal growth form: Lovett Doust 1981). Carson and colleagues (Carson and Pickett 1990, Carson and Root 2000, Banta et al. 2008) extended this hypothesis by providing compelling experimental evidence that competition was the actual mechanism that promoted dominance: the ability of *Solidago* to cast deep shade restricted all other species as subordinates. However, they neglected to consider alternative mechanisms (e.g., herbivore

resistance or rapid clonal spread).

Classical theory predicts that niche differences allow coexistence – thus co-occurring species should exhibit tradeoffs along critical axes: competition, colonization, growth rate, herbivore resistance and herbivore tolerance. Furthermore, we propose that differences in life-history traits, such as the degree of herbivore resistance, competitive ability or their covariance, will underlie community dynamics and coexistence. Our goal was to identify the traits and trait combinations that would predict or explain the repeated dominance of *So. canadensis* in thousands of old-fields. Old-fields in the United States and southeastern Canada have light-limited understories, with moderate to high soil resource availabilities (Bazzaz 1996); thus, we hypothesized that species that allocate relatively more to growth, light attenuation, and herbivore tolerance should be more abundant, relative to species allocating more to colonization and herbivore resistance (Coley et al. 1985, Tilman 1988, 1990a). We also hypothesized that the dominant *So. canadensis* would be the superior competitor specifically in terms of its ability to grow by slow dense clonal spread (the phalanx) thereby it casts deep shade (Carson and Pickett 1990, Bazzaz 1996).

2.2 MATERIALS AND METHODS

2.2.1 Overview

We conducted these experiments near the Pymatuning Laboratory of Ecology in northwestern Pennsylvania (Meadville, PA). We used nine old-field plant species that vary in their abundance

from being typically dominant to those typically rare; seven herbaceous composites: *Euthamia gramifolia, Solidago canadensis, So. gigantea, So. rugosa, Symphyotrichum novae-angliae, Sy. pilosum*, and *Sy. prenanthoides*; one shrub: *Cornus racemosa;* one naturalized grass: *Elymus repens*. Some of these species differ sharply in architecture (compare *C. racemosa* versus *El. repens*), and the goldenrods (*Solidago* and *Euthamia*) differ fairly substantially from the New World asters (*Symphyotrichum)* (Bazzaz 1996). However, we purposely chose 3 *Solidago* species that share similar architecture and niche, yet vary consistently in abundance. All of these species commonly co-occur, (Banta et al. 2008) and were chosen from a pool of over one hundred coexisting species in northeastern old-fields (e.g., Meiners et al. 2007). Despite this diversity, our focal species make up over 60% of typical old-field groundcover (Pendergast, unpublished data). *So. canadensis* consistently dominates these old-fields regardless of species composition, though *Sy. pilosum* and other asters are typically abundant early in succession (Carson and Root 1999, Banta et al. 2008).

2.2.2 Do old-field plant species exhibit classic investment tradeoffs?

To evaluate the critical traits and tradeoffs that may maintain diversity and inform patterns of dominance and relative abundance in old-fields, we established and maintained long-term monocultures, manipulated insect and mammalian herbivores, quantified key traits, and conducted a separate resource suppression (shade tolerance) experiment.

Establishing monocultures and implementing herbivore treatments. We established monocultures in 2000 by planting six seedlings (from at least 3 local source populations) on freshly tilled soil in the center of 4 x 4 m plots in an old-field. Species were randomly allocated to plots in five blocks, with four plots of each species in each block for a total of 180

monocultures. Each species was allowed to spread clonally and plots were weeded to eliminate heterospecifics and any conspecifics that colonized by seed.

Four treatments were randomly allocated to each species: fences to exclude mammals, insecticide application to exclude insect herbivores, insecticide application x mammal exclusion and an unmanipulated control. Fences were 2 m high and the mesh was small enough to exclude rabbits and woodchucks. We applied a broad-spectrum synthetic pyrethroid insecticide, es-Fenvalerate (Dupont, USA) every 7 to 10 days during the growing season (Carson and Root 2000, Siemann et al. 2004).

Measuring traits. The monocultures were allowed to fully develop for 5 years reaching a quasi-equilibrium where stem densities in the center of these plots remained relatively constant (Pendergast unpublished data). In June and August of 2005, we measured plant heights and % leaf damage via herbivores of 3 leaves of 10 haphazardly-chosen individuals in each plot (Carson and Root 2000). We also measured total area of the monoculture and light attenuation with Li-Cor line quantum sensors (1 m x 1 cm, see Stevens and Carson 2002, Banta et al. 2008).

Trait definitions. Long-lived old-field perennials vary in their ability to cast shade (Banta et al. 2008). Old-field species that cast deep shade suppress coexisting species and experimentally increasing light into the understory causes increases in species richness (Carson and Pickett 1990, Carson and Root 2000). Consequently, one key metric of competitive ability in these communities is the relative ability of these species to cast shade or draw down light (Banta et al. 2008). Thus, our measures of light extinction (100 - % light at soil surface) in the absence of herbivory serve as one key and well accepted metric of competitive ability, both theoretically and empirically (Carson and Pickett 1990, Canham et al. 1994, Huisman and Weissing 1994, Huisman et al. 1999, Carson and Root 2000, Passarge et al. 2006, Vojtech et al.

2007, Banta et al. 2008). We acknowledge that soil resources may also be limiting (Carson and Barrett 1988, Carson and Pickett 1990), but experimental additions of these resources typically allow old-field species to cast even deeper shade (Carson and Pickett 1990). We used final monoculture area, after five years of clonal spread without herbivores, to quantify colonization into open habitat. This is appropriate as the vast majority of recruitment in old-fields is almost strictly clonal after three years of abandonment (Bazzaz 1996).

We used the amount of undamaged leaf tissue (100 - % herbivore damage) on different plant species in plots with herbivores present as a metric of resistance whereby the more insect damage sustained the lower the resistance (operational resistance; Mauricio 2000, Agrawal 2004, Banta et al. 2008). Finally, we define tolerance as one minus the relative change in height between control and total herbivore exclusion plots (Rausher 1992, Fineblum and Rausher 1995, Mauricio et al. 1997). Stem height is highly correlated with aboveground biomass for these species (Bazzaz 1996). We fully acknowledge that operational tolerance is complicated by differential damage levels across species.

Shade tolerance experiment. To quantify the ability to survive resource suppression (i.e., shade), we conducted a shade frame experiment with a subset of our species (*So. canadensis*, *So. gigantea*, *Sy. novae-angliae*, and *Sy. pilosum*). Using open frames and 9 varying densities of shade cloth, we established a continuum of light availability (average light availability for each shade level: 67.8% (open frame), 39.3%, 21.2%, 17.7%, 14.3%, 7.3%, 4.1%, 3.8%, 3.5%, 0.0002%). Each shade level was replicated 5 times, with 50 total shade frames. Beginning in June 2004, 3 week-old seedlings were transplanted individually into 2.8L pots filled with local topsoil. Each frame contained one of each species and was watered regularly. Plants grew in these frames for 72 days, with mortality recorded every two weeks.

Data analysis. All analyses were conducted in SAS 9.2 (Cary, NC) using the Proc Mixed procedure. We regressed plot averages for appropriate traits for each hypothesis, using Block as a random variable. We only regressed plot averages for all species and treatments for the predicted competition-colonization tradeoff. All other hypotheses were tested using plot averages from the appropriate treatments (e.g., growth rate from all herbivores excluded treatment). To satisfy assumptions of normality, light extinction and resistance values were square-root transformed and we took the natural log of colonization values (Sokal and Rohlf 1995). To test if a tradeoff exists between light reduction and shade tolerance, we regressed plot averages of light extinction against the polynomial slope of plant survivorship with light availability.

2.2.3 Can traits and tradeoffs predict relative abundance?

Estimating relative abundance. We quantified relative abundance of our focal species using published and local empirical data, the latter especially for rarer species. Banta et al. (2008) conducted a thorough examination of published relative abundances of many old-field plant species. However, they did not present data on *Cornus racemosa, Elymus repens*, or *Sy. prenanthoides*. Although other studies have found these species (e.g., Mellinger and McNaughton 1975, Stover and Marks 1998), in 2005 we conducted an additional census to confirm their abundance in a local, mid-successional field. We established 40, 2x2 meter plots in this old-field, with 2-meter buffers along 5 transects. We measured species-specific cover in all plots, dividing a species' cover by the total sum cover in each plot. Although we identified all nine of our species in this old-field census, we have only incorporated abundance data from *C. racemosa, El. repens,* and *Sy. prenanthoides*. We feel it best to rely on the published data (Banta

et al. 2008) as it encompasses almost two dozen fields of varying ages across the Midwestern and Northeastern United States. If traits and trait combinations can predict relative abundance, then it is far more conservative to contrast these values against average species abundance across spatial and temporal scales, rather than a single adjacent field.

Collapsing traits using PCA. To test the hypothesis that specific trait combinations can predict relative abundance and inform dominance, we used principal component analyses to collapse trait variation and subsequently regress PCA values against relative abundance data. Because multiple traits are likely to be correlated with each other and potentially indicate spurious conclusions, we used Proc Factor in SAS 9.2. Values for competition, colonization, herbivore resistance, herbivore tolerance, and growth (as above) were included. Principal components were then regressed against relative abundance values using Proc Mixed (Hovick et al. 2012).

2.3 RESULTS

2.3.1 Little evidence for tradeoffs in critical life history traits

1. Competition-Colonization: To our surprise, we found a strong positive relationship between competition and colonization ability (i.e., extent of clonal spread) across all species and treatments (Figure 2.1 A, $p = 0.0002$, $r^2 = .066$). This is the exact opposite of what theory predicts. In fact, species that cast deep shade also had the most rapid clonal spread in terms of spatial extent. However, in plots protected from herbivory, this relationship disappeared ($p = 0.226$, Figure 2.1B). Most importantly, the dominant species was the best colonizer *and* the

best competitor (*So. canadensis*), regardless of herbivory (Figure 2.1A,B). While some species did fall along the predicted competition-colonization tradeoffs (*C. racemosa, El. repens, Eu. gramifolia, So. rugosa,* and *Sy. prenanthoides*), the remaining four species did not, being poor colonizers *and* poor competitors (e.g., *Sy. novae-angliae*).

2. Competition-Herbivore Resistance: We found no evidence of the predicted tradeoff between competitive ability and herbivore resistance (p =0.425, Figure 2.2A). *El. repens* and most asters were both poor competitors and poorly herbivore resistant. *Solidago* species and the shrub *Cornus*, in contrast, were good competitors (cast deep shade) and suffered little herbivore damage.

3. Colonization-herbivore resistance: We found no evidence of tradeoff between herbivore resistance and colonization (p =0.2372, Figure 2.2B). Although a few species adhered to classical predictions (*C. racemosa, So. rugosa,* and *El. repens*), the asters (*Symphyotrichum)* in general were poor colonizers and poorly resistant. In contrast, three goldenrod species were both highly herbivore resistant and clonally spread the fastest, particularly *So. canadensis*.

4. Growth rate-herbivore resistance: We found no evidence of the predicted tradeoff between growth and herbivore resistance (p = 0.6968, Figure 2.2C). In fact, the fastest growing species, the *Solidago* species, was also one of the most resistant. In contrast, *Sy. prenanthoides* and *El. repens* were the slowest growing and suffered high herbivore damage. This lack of pattern remained even when *C. racemosa*, the only woody species, was excluded (p = 0.4842) or substituted the average annual growth rate of *C. racemosa* (p=0.8701).

5. Herbivore resistance-tolerance: We found no evidence of the predicted tradeoff between herbivore resistance and tolerance ($p = 0.8761$, Figure 2.2D). However, this lack of pattern appears to be driven by the goldenrods. *Euthamia* and all *Solidago* species experienced low rates of herbivore damage in the presence of herbivores and small differences in biomass between protected and unprotected plots (high operational tolerance). Indeed, by excluding goldenrod species from this analysis, we do see a trend of the predicted negative correlation between herbivore damage and tolerance across the aster, grass, and shrub species ($p = 0.0947$, $r^2 = 0.1251$).

6. Mechanisms of Competition: We found no evidence for a tradeoff between resource competitive response and effect. Instead, we found strong support that species that cast the deepest shade (competitive effect) are also the most shade tolerant (competitive response). This pattern holds true for light extinction measured only where herbivores were removed (Figure 2.3, $p = 0.0135$, $r^2 = 0.8359$) or in all treatments ($p = 0.0076$, $r^2 = 0.7103$).

2.3.2 Traits predict relative abundance

To evaluate whether traits and trait combinations can accurately predict the relative abundance of species within a community, we collapsed trait data into principal components and regressed PCA values against estimates of species relative abundance. We identified two principal component factors, with Factor 1 heavily loading growth, resistance, and competitive ability values (Appendix 2.1). Colonization and tolerance primarily loaded on Factor 2. Factors 1 and 2 explained 57.5 and 42.5 percent of trait value distribution, respectively.

We found a significant relationship between trait PCA values and estimates of relative abundance ($p < 0.0001$, Figure 2.4), explaining 39.55% of the variation in relative abundance.

Both PCA Factor 1 and Factor 2 accurately predict relative abundance ($p = 0.0004$, Figure 2.4A, $p = 0.0015$, Figure 2.4B, respectively). In general, this model predicts that more abundant species are likely to have faster growth rates, reduce light to low levels, colonize territory quickly, tolerate herbivory and incur low amounts of herbivore damage.

2.4 DISCUSSION

2.4.1 Overview

The vast majority of coexistence theory is foundationally based on among species tradeoffs in allocation, phenology, morphology, physiology or life history. However, numerous theoreticians have discussed the possibility of species that can violate these predictions. Tilman and Rosenzweig identified the potential for a "superspecies", "supercompetitive species", or "super-hero phenotypes" (Tilman 1982, 1988, Rosenzweig 1995). Kneitel and Chase (2004) dubbed such species the "Hutchinsonian demon":

> *"whereby one species in a community dominates because it is the best at colonizing new patches, utilizing all the resources, avoiding predators and resisting stresses"*

Here, we present evidence that *Solidago canadensis* is such a species because it was the superior competitor for light (cast deep shade), survived in deep shade, spread the furthest clonally, was highly herbivore resistant, highly herbivore tolerant, and had the fastest growth rate (Figures 2.1, 2.2, 2.3). These traits would allow this species to rapidly acquire occupied and unoccupied space, hold territory and suppress competitors by casting deep shade, and be nearly

immune to enemies. We argue that our results answer the question why this species dominates old-fields over nearly half a continent of old-fields (Bazzaz 1996, Banta et al. 2005). Thus, this species is robust to changes in key site factors (fertility, co-occurring species, herbivore abundance) that might favor competing species.

Indeed, eutrophication causes a substantial increase in its dominance (Carson and Barrett 1988, Carson and Pickett 1990). Most importantly, we found that a single species can be the superior competitor, the best colonizer, and immune to its enemies *relative to the species it co-occurs with*. While our findings may fly in the face of much of ecological theory, the fact that *Solidago canadensis* dominates over such a vast geographic area suggests that it may have a unique suite of traits that promotes its dominance. We, of course, do not deny that large woody species eventually displace goldenrods from old-fields. Nonetheless, goldenrods, and particularly *So. canadensis*, have a superior suite of traits that allow them to be the dominant species over more than 100 herbaceous species that they coexist with. Moreover, goldenrods can delay succession for decades (Meiners et al. 2007) and they remained the dominant or co-dominant species even following a severe insect outbreak of a specialist enemy (Carson and Root 2000). In fact, the conversion of old-fields from the goldenrod-dominated stage to a woody species stage may require an insect outbreak (Carson and Root 2000).

2.4.2 Hutchinsonian Demons?

One critique of our results is that we failed to consider other key tradeoffs. This is undoubtedly true, and other critical, unmeasured and possibly unpredicted tradeoffs may operate within these systems (Suding et al. 2003, Harpole et al. 2011). Tradeoffs are also likely to change rapidly across abiotic and biotic gradients and with temporal and spatial scale. However,

here we examined 6 tradeoffs, all of which were expected to operate and well supported within the literature. More importantly, if multiple classic tradeoffs sequentially fail, it becomes almost impossible to falsify the hypothesis that tradeoffs structure this community.

However, the ability to avoid critical life history tradeoffs begs the question: how? All organisms have limited resources to allocate to growth, reproduction, and defense. Species may deviate from predicted tradeoffs via overlooked tradeoffs, correlated traits, and unequal resource constraint. Goldenrods may experience considerable but unmeasured tradeoffs, such as drought resistance, resource co-limitation, or clonal vs. sexual reproduction. Indeed, *So. canadensis* can be drought and nitrogen limited (Carson and Pickett 1990), but even under severe drought condition still be "common and conspicuous species of low prairies" where it sometimes forms dense stands (50 stems/m^2) that apparently shade out the majority of competing grasses (Weaver and Fitzpatrick 1934 pg. 236, see also Weaver 1958). Goldenrods do not appear to tradeoff on sexual reproduction allocation (Abrahamson et al. 2005), and among our species, have the smallest wind-dispersed seeds (Appendix 1.1). Goldenrods may also have unpredicted linked traits, such that the dense phalanx clonal growth will cast deep shade in a light-limited system, but also allow an overlapping, marching front, thus rapidly acquiring territory. Finally, we feel the most likely, but not-mutually exclusive, explanation is a flawed assumption of similar resource constraint (Stearns 1989, Viola et al. 2010). The densely packed, interconnected ramets of *So. canadensis* subsidize 360 degree colonization into competitor territory and mitigate soil resource heterogeneity (Hartnett and Bazzaz 1985). These ramets form a rolling photosynthetic block, overtopping neighbors, denying light to its competitors, and penetrating competitors' territory; this results in vast carbon acquisition, relative to other species. The substantially greater acquisition of

resources may allow seemingly impossibly allocation compared to co-occurring, but resource-poor species.

If *So. canadensis* is such a Hutchinsonian demon, how can it coexist with 80+ species for decades or more (Meiners et al. 2007)? Theory predicts that the species with superior abilities to compete, colonize, and mitigate herbivores should eventually drive subdominant species to local extinction. However, the Achilles heel of goldenrods may be its susceptibility to herbivore outbreak. Outbreaks of insect herbivores, such as chrysomelid beetles, every 15 or more years can drastically reduce goldenrod biomass, survivorship and reproduction, and substantially increased light penetration (Root and Cappuccino 1992, Carson and Root 2000). This release from resource competition results in long-term increased biomass and diversity of subdominants – even though *So. canadensis* remained the dominant species. Moreover, this may be the switch that allows rapid tree invasion, and thus this otherwise stalled succession is allowed to proceed with forest species recruitment (Carson and Root 2000).

Our findings suggest an intriguing possibility of how Hutchinsonian Demons are regulated; large-scale enemy outbreaks that occur periodically and act as a keystone species. However, this dynamic would play itself out over extremely long time periods and huge spatial areas: this is, in fact, exactly what occurs in boreal forests and also other biomes (Carson et al 2004). For example, insect herbivore outbreaks cause increasing mortality of balsam fir (*Abies balsamea*) as the host increases in relative abundance and becomes dominant (Begeron & Leduc 1998). Periodic herbivore outbreaks may frequently go unnoticed, but if outbreaks primarily reduce the fitness of the dominant species, they can promote coexistence (Carson and Root 2000, Carson et al. 2004, Allan and Crawley 2011). Indeed, these are the very predictions of Host Concentration theory and parallels with the Janzen-Connell hypothesis: increasing densities of a

host leads to increased susceptibility to natural enemies (Janzen 1970, Connell 1971, Long et al. 2003, Carson et al. 2004, Carson et al. 2010).

2.4.3 Are there other Hutchinsonian niches?

Rather than being the exception that proves the rule, the ability to avoid critical tradeoffs may be a reliable explanation for stable dominance in systems worldwide. Dominance is certainly not uncommon within plant communities, occurring from boreal forest through the tropics (Carson et al 2004). The ability to overcome a single overarching tradeoff that regulates species within a trophic level may be sufficient to rapidly alter relative abundance and community structure. For example, threetip sagebrush (*Artemisia tripartita*) is dominant over 3.4 million hectares throughout the northern Rocky Mountains and Great Basin in western North America (Bork et al. 1998). Sagebrush is generally highly resistant to ungulate herbivory (Beetle 1960), highly drought and fire tolerant (Daubenmire 1972, Akinsoji 1988), and can become nearly monodominant after fire (Passey and Hugie 1962, Royo & Carson 2005). Perhaps by avoiding herbivore, fire, and drought tradeoffs, sagebrush can domiante huge swaths of western Canada and United States. Similarly, the dramatic increase in the abundance of red maple (*Acer rubrum*) and other shade- and browse tolerant hardwoods (*e.g.*, *Fagus grandifolia*) in the eastern United states may indeed be caused by a century of anthropogenic suppression of their Achilles heel: fire (Abrams 1998, Nowacki and Abrams 2008).

2.4.4 Implications for invasive species

Our results suggest that we may require a paradigm shift for *apriori* targeting of potential invasive species. The current focus is on a small number of tradeoffs on a single axis: herbivore resistance and growth/competitive ability (e.g., Enemy Release and the Evolution of Increased Competitive Ability (Blossey and Notzold 1995, Keane and Crawley 2002). Alternatively, predictions for plant invasion often focus on single traits such as those associated with weedines or novel weapons (reviewed in Theoharides & Dukes 2007). Perhaps we should be most worried about species that have a suite of traits that may allow them to dominate over large areas. This fits well with strong evidence that species that are abundant and distributed over a wide geographic area are more likely to become invasive (Goodwin et al. 1999, Pyšek et al. 2009, Hovick et al. 2012)

In fact, *So. canadensis* has become a highly successful invasive species in temperate zones world-wide, dominating disturbed and herbaceous habitats in Europe, Asia, Russia, Australia, and New Zealand (Weber 2000, 2001, 2003, Dong et al. 2006, Lu et al. 2007).

As *So. canadensis* is already highly herbivore resistant and tolerant, its invasion is unlikely to be attributed to a release from natural enemies. Indeed, the robust study by van Kleunen and Schmid (2003) failed to detect evidence of enemy release or the evolution of improved competitive ability in invasive and native *So. canadensis* genotypes. Instead, the *So. canadensis* phenotype has evaded the critical tradeoffs that constrain other species, making it a jack-of-all-trades, the master of all, and a true Hutchinsonian demon.

2.4.5 Conclusions and Implications

Identifying the critical traits and tradeoffs can provide insight into community assembly and coexistence across and within habitats (Keddy 1992, Leibold 1998, Chase et al. 2002, Clark et al. 2003, HilleRisLambers and Dieckmann 2003, Kneitel and Chase 2004, Cornwell and Ackerly 2009, Viola et al. 2010), and drivers of relative abundance (Levine and Rees 2002, Suding et al. 2003, Fargione and Tilman 2006, Cornwell and Ackerly 2010). These tradeoffs are likely to change across gradients (e.g., Cornwell and Ackerly 2009), temporal and spatial scale (Chesson and Warner 1981, Chesson 2000, Clark et al. 2003, Kneitel and Chase 2004, Calcagno et al. 2006, Cadotte 2007a), and may not be classically predicted (Suding et al. 2003). Key traits and tradeoffs may also play an important applied role: predicting probable invasive species and explaining other dominant species. Some have concluded that invasive species are simply 'better' at crucial processes than indigenous species, thus facilitating their spread (Crawley et al. 1996, Pyšek and Richardson 2007). Indeed, a majority of studies found invasive species to have greater colonization, reproduction, growth, and herbivore resistance, among other traits, than related native taxa (also see Rejmánek and Richardson 1996, Baruch and Goldstein 1999, Thuiller et al. 2006, Grotkopp and Rejmánek 2007, reviewed in Pyšek and Richardson 2007). Fitting this model, *Solidago canadensis* is an exotic invasive species overseas and form highly productive, low-diversity stands in both Europe and Asia where they slow down forest succession and decrease land values (Weber 1998, 2001, Ding et al. 2006). Predictive invasive tradeoffs may be commonplace, but largely unexplored. For example, North American *Centaurea maculosa* genotypes are larger and better defended than their European ancestors (Ridenour et al. 2008) and *Acer platanoides*, invasive in the northeastern USA, have both high growth rates and high survivorship (Martin et al. 2010) while being more light, water, nitrogen

and phosphorus efficient than its native congener (Kloeppel and Abrams 1995). Most telling, perhaps, is the evolution of greater nitrogen allocation to photosynthetic machinery, at the expense of structural defenses, in invasive *Ageratina adenophora* genotypes (Feng et al. 2009). If species are released from key tradeoffs, such as specialist herbivory, they can then allocate those resources towards other traits.

The assumption that a single (or few) tradeoffs can mediate local coexistence in nature is likely overstated, if not erroneous (Clark et al. 2003). However, patterns of allocation and physiology scale from organismal traits to demographic, community, and ecosystem processes (Lavorel and Garnier 2002, Suding et al. 2003, McGill et al. 2006). These trait and tradeoffs inform which crucial processes structure a community, and may provide the key to predicting relative abundance and invasion.

2.5 ACKNOWLEDGMENTS

We are grateful to Jill Anderson, Charles Mitchell, James Cronin, and Deborah Goldberg. We thank Garland Waleko and Bryan Anderson for their field assistance. This work was funded by the G. Murray McKinley Research Fund of the Pittsburgh Foundation, a NSF Doctoral Dissertation Improvement Grant (#0508012) and the Corning Institute for Education and Research.

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2.6 FIGURES

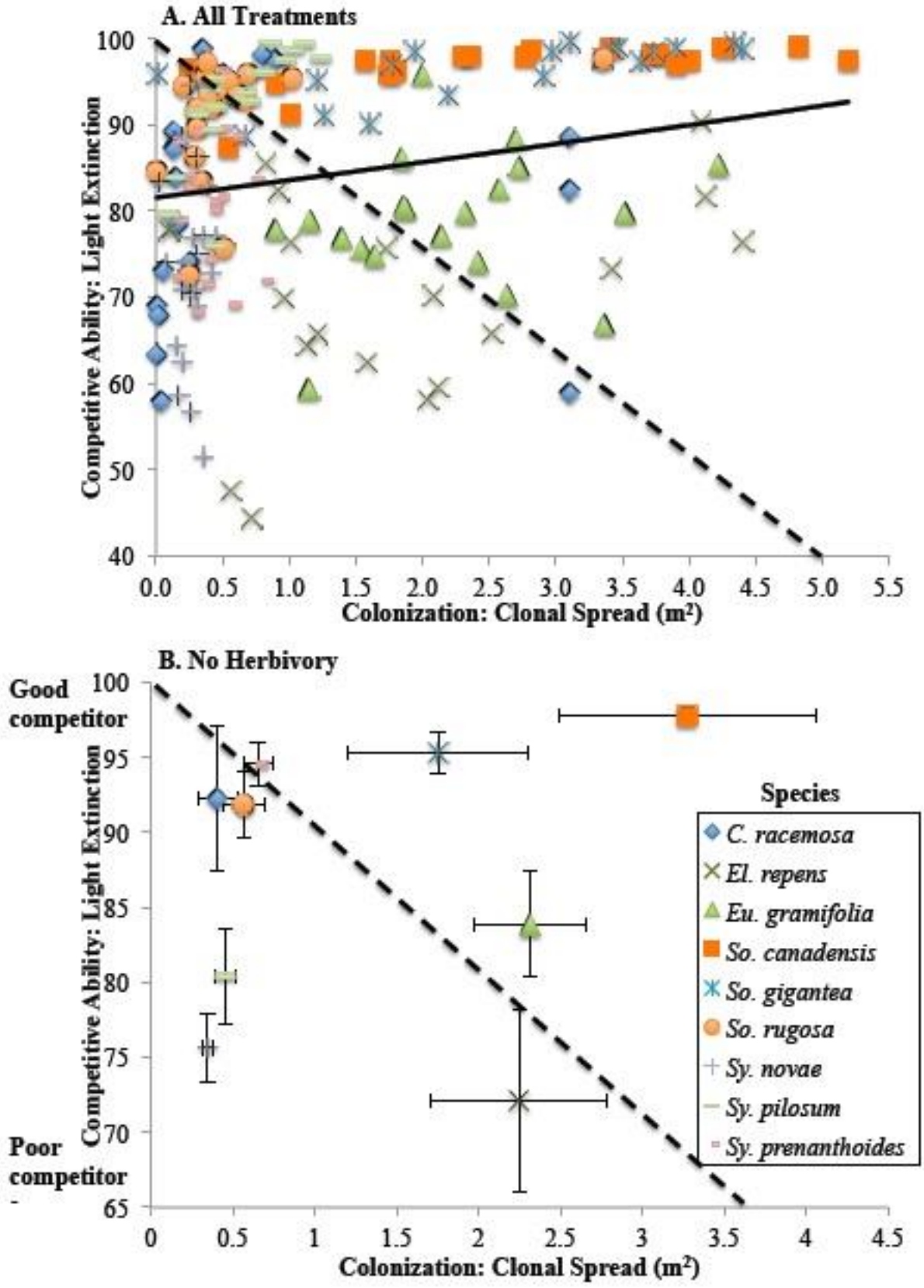

A. All Treatments
Competitive Ability: Light Extinction
100
90
80
70
60
50
40
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
Colonization: Clonal Spread (m²)
B. No Herbivory
Good competitor
Poor competitor
Competitive Ability: Light Extinction
100
95
90
85
80
75
70
65
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Colonization: Clonal Spread (m²)
Species
C. racemosa
El. repens
Eu. gramifolia
So. canadensis
So. gigantea
So. rugosa
Sy. novae
Sy. pilosum
Sy. prenanthoides

Figure 2.1. Relationship between competitive ability, as defined by light extinction, and colonization (clonal spread) of nine old-field plant species. Dashed lines represent predicted trade-off. **A.** Light attenuation and clonal spread of all plant species from all treatments. Although classical theory predicts a tradeoff between competitive and colonization ability, we found a positive relationship between these traits ($p = 0.0002$), indicating that the best colonizers also drew down light to lower levels. **B.** We found no relationship between these traits in plots completely excluded from herbivory. However, *So. canadensis* remains the best colonizer and best competitor in the absence of herbivory.

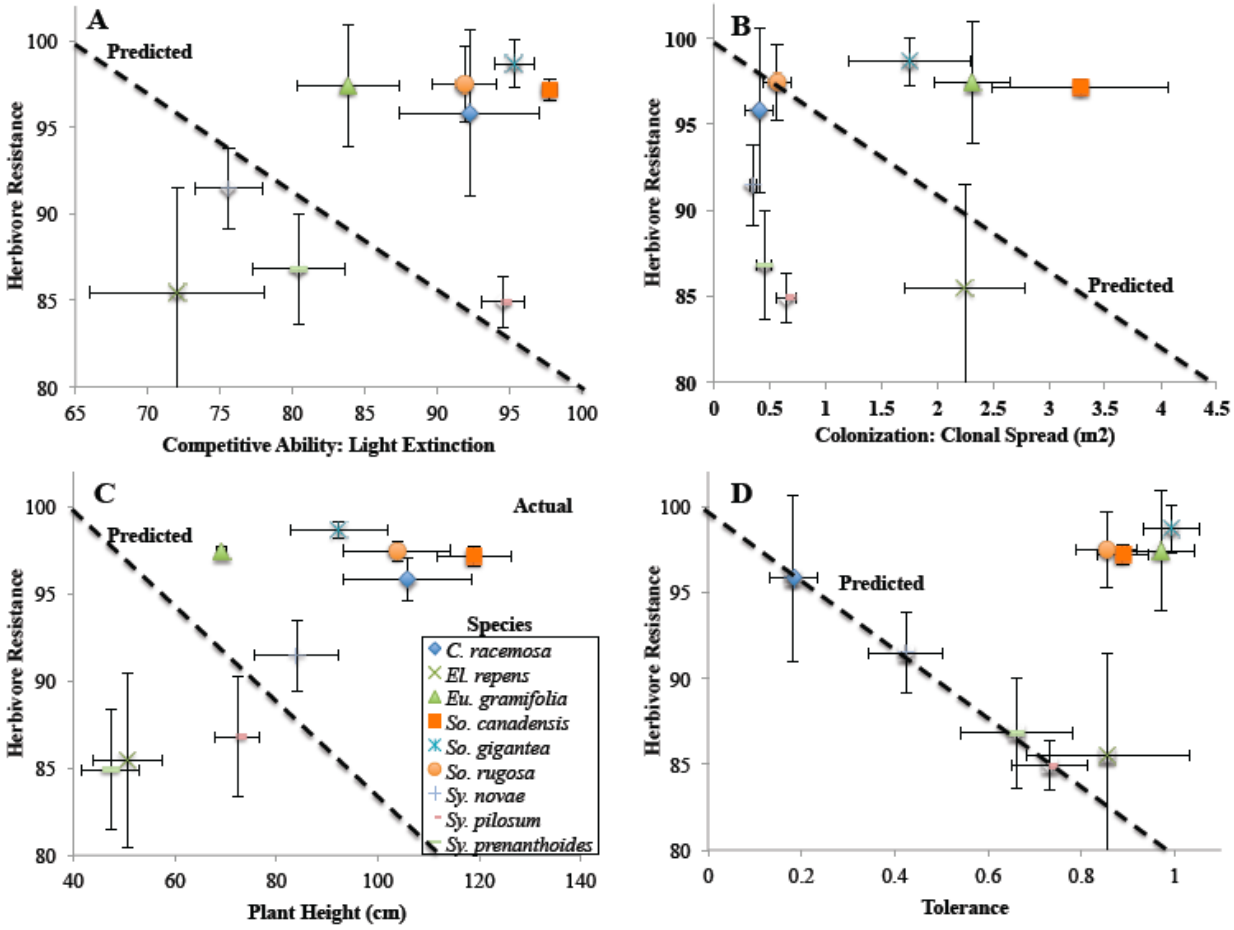


Figure 2.2. Classic trait tradeoffs between herbivore resistance, herbivore tolerance, colonization, and growth in nine old-field plant species. Dashed lines represent predicted relationships. **A.** Relationship between herbivore resistance (100 - % leaf damage) in the presence of herbivores and the ability to drawn down light (100 - % ambient light at soil surface) with herbivores removed. **B.** Relationship between herbivore resistance and clonal spread in the absence of herbivory. **C.** Relationship between herbivore resistance and plant growth in the absence of herbivores. **D.** We found no overall relationship between herbivore resistance and herbivore tolerance ($p=0.8761$), but goldenrods were significantly different from other species ($p=0.027$).

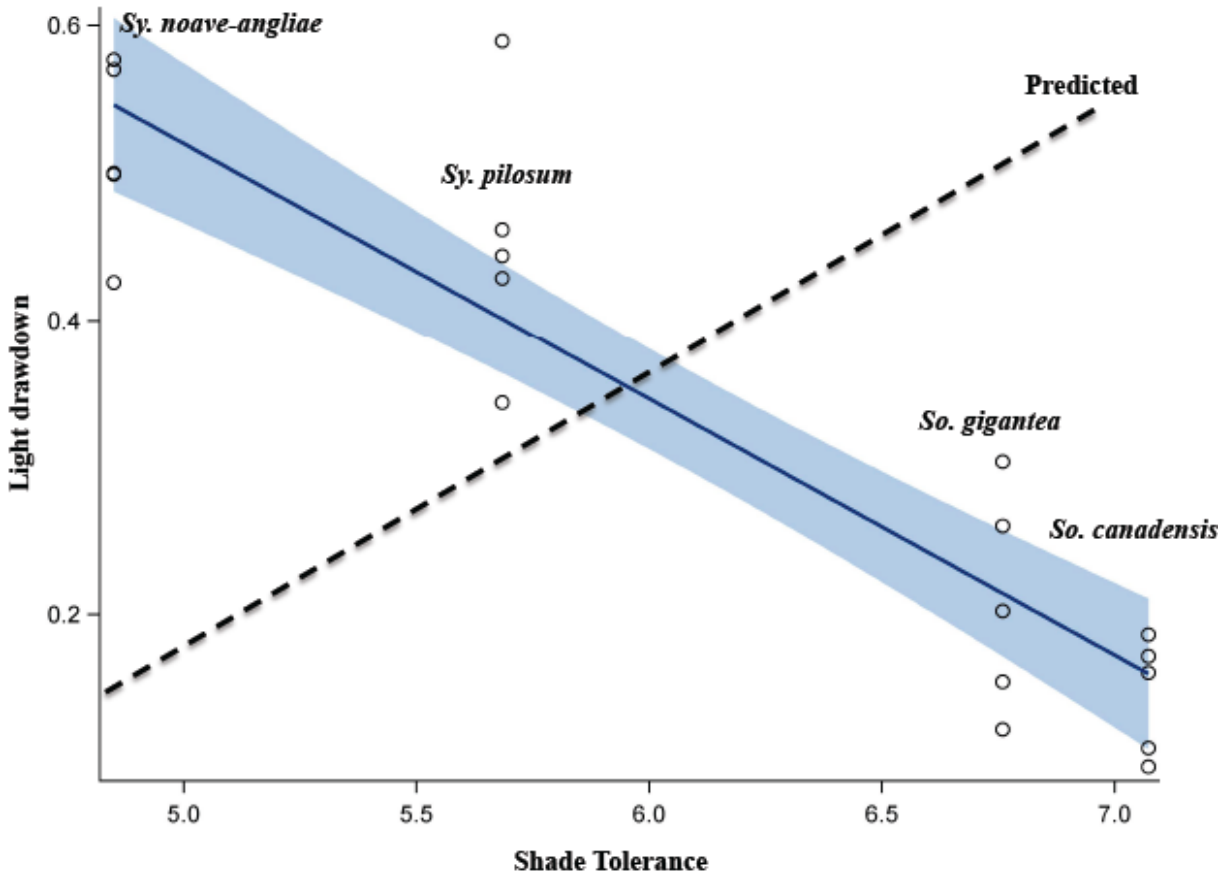
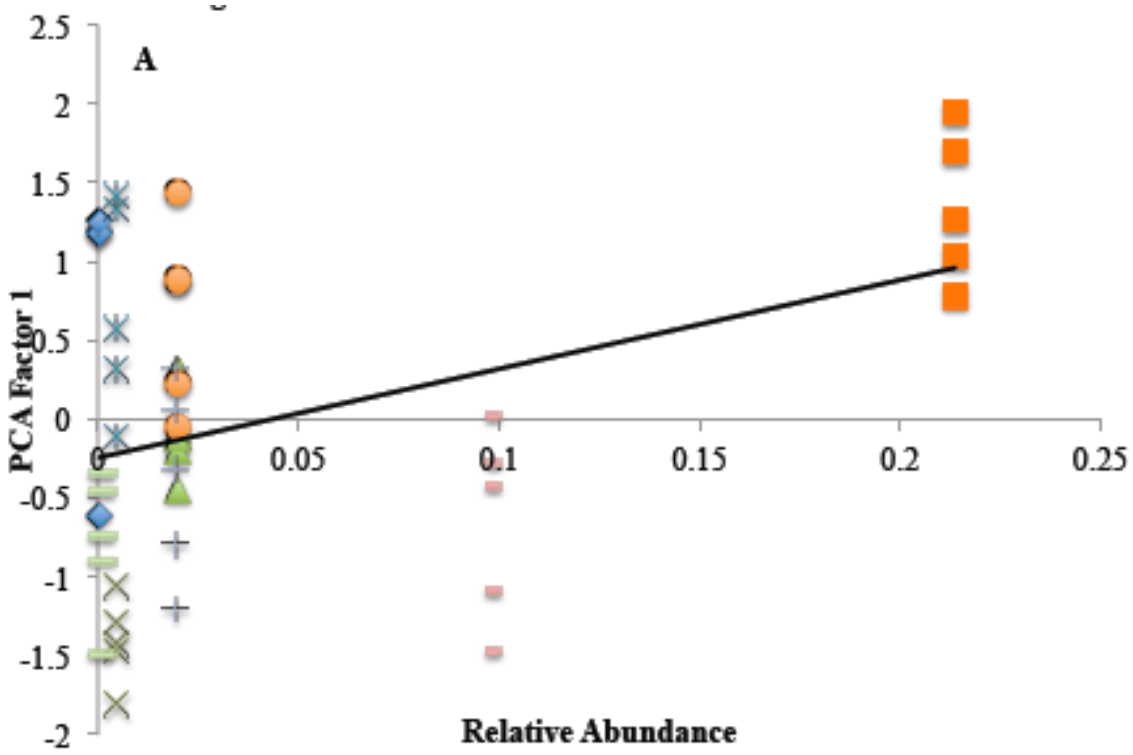


Figure 2.3. Lack of trade-off in 4 old-field plant species between mechanisms of competitive ability: resource drawdown and low resource tolerance. Contrary to theoretical predictions (dashed line) we found a significant positive relationship between resource drawn and shade tolerance ($p = 0.0076$). Shading represents confidence limits for mean predicted values. *So. canadensis*, the dominant species, drew down light to the lowest levels and had the greatest survivorship with decreasing light availability.


A
PCA Factor 1
Relative Abundance
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
0.05
0.1
0.15
0.2
0.25

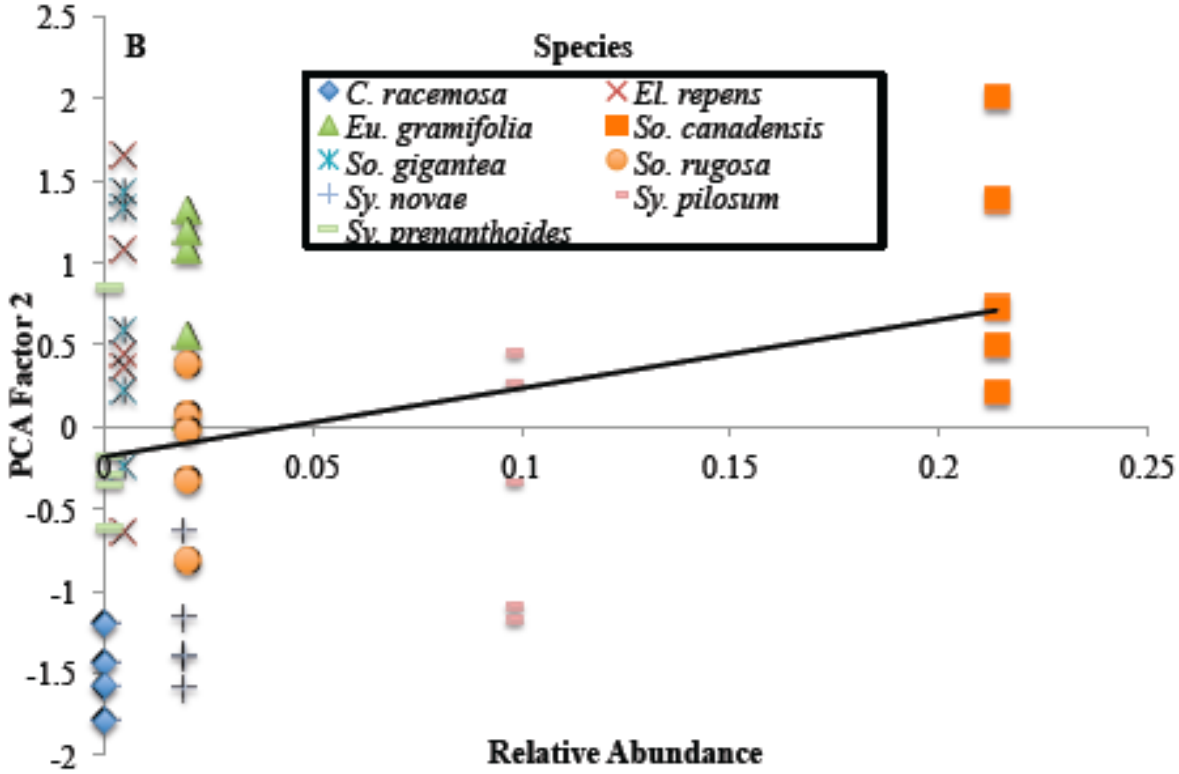

B
Species
C. racemosa
El. repens
Eu. gramifolia
So. canadensis
So. gigantea
So. rugosa
Sy. novae
Sy. pilosum
Sy. prenanthoides
PCA Factor 2
Relative Abundance
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
0.05
0.1
0.15
0.2
0.25

Figure 2.4. Back-transformed relative abundance of 9 old-field plant species regressed against trait-based PCA Factors 1 (A) and 2 (B). **A.** PCA Factor 1 is strongly positively weighted by plant height and negatively weighted by herbivore damage and light draw down ($p= 0.0004$). **B.** PCA Factor 2 is strongly weighted by herbivore tolerance and clonal colonization, and is also predictive of relative abundance ($p= 0.0015$). This model predicts that more abundant species are more likely to be taller, strongly reduce light levels, colonize rapidly, incur low amounts of herbivore damage, and tolerate herbivory.

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3.0 BELOWGROUND BIOTIC COMPLEXITY DRIVES ABOVEGROUND DYNAMICS: A TEST OF THE SOIL COMMUNITY FEEDBACK MODEL

3.1 INTRODUCTION

Although soil organisms have had known dramatic impacts on agronomic plant species for centuries (de Bary, 1861) if not millennia, they have only recently been incorporated into ecological theory (e.g., Bever *et al.*, 1997; Bever, 2003). Recent ecological studies provide compelling evidence that plant-soil feedbacks are common and may drive patterns of plant performance, relative abundance, community dynamics, and exotic invasion (Klironomos, 2002; Kardol *et al.*, 2006; Mangan *et al.*, 2010). However, the relative importance of soil community feedbacks and their impact on key plant community interactions is largely unknown. Here we test the predictions that lie at the heart of this relatively new body of theory. ***1. The Plant Feedback hypothesis***: plant species "culture" their own specific microbial and microzoan community within their rhizosphere which influences the performance of con- and heterospecific plants (Bever *et al.*, 1997). ***2. Feedbacks and Competitive Hierarchy hypothesis***: the development of contrasting soil communities alters plant performance sufficiently to change the competitive hierarchy and thus population dynamics of coexisting species (Bever, 2003).

Local feedback interactions potentially scale up to drive patterns of relative abundance; specifically, positive feedbacks may increase plant abundance. In two landmark studies, rare

species suffered more from negative feedback than common species in both temperate and tropical systems (Klironomos, 2002; Mangan *et al.*, 2010). Plant-soil feedbacks are therefore likely to contribute to observed patterns of density dependence and species abundance (i.e., Janzen-Connell effects, Janzen, 1970; Connell, 1971; Petermann *et al.*, 2008; Mangan *et al.*, 2010). If these processes are indeed as pervasive and strong as the literature suggests, plant-soil feedbacks may typically modify species interactions and drive community dynamics and dominance.

Understanding the extent and strength of plant-soil community dynamics is critical to identify mechanisms that determine plant competitive outcomes, relative abundance, and coexistence (Bever, 2003). Overall, little is known about belowground soil communities and their general roles in driving plant community dynamics. This is certainly understandable given the staggering diversity in belowground communities; a single cubic centimeter of soil can harbor over 6000 species of microorganisms (Torsvik *et al.*, 2002). Although plant species can culture distinct belowground communities, e.g., rhizosphere bacteria, pathogens and arbuscular mycorrhizal fungi (Westover *et al.*, 1997; Vandenkoornhuyse *et al.*, 2003), this is not always the case (see Burke & Chan, 2010). Currently it remains unknown how frequently plants culture distinct and species-specific belowground communities, especially in the field. More importantly, however, it is unclear the degree to which soil communities, distinct or not, benefit or harm their hosts. Nonetheless, results to date indicate that feedbacks are often negative (Bever, 1994; Reinhart *et al.*, 2003; Kulmatiski *et al.*, 2008) and thus plants, especially rare native species, culture communities through time that are inimical to themselves (Klironomos, 2002; Mangan *et al.*, 2010).

Even less is known regarding the degree that plant-soil feedbacks alter competitive

relationships, yet this goes to the core of whether these feedbacks drive community dynamics. Bever (1994) found no effect of soil communities on competitive interactions, whereas other studies found compelling evidence to the contrary (Casper & Castelli, 2007; Kardol *et al.*, 2007). Here we build upon these studies using an experimental approach that explicitly manipulates biotic soil communities and controls for abiotic effects. Perhaps most importantly, we ask whether changes in competitive interactions via plant-soil feedbacks can alter hierarchies and population projections.

We use this framework to gain insight into a long-standing pattern in ecology – the dominance of goldenrods (primarily *Solidago canadensis*) over dozens of other species in northeastern and mid-western US old-fields (Bazzaz, 1996; Carson & Root, 2000). Soil community feedback theory predicts that consistently abundant species may be maintained by more positive feedbacks, relative to other species. Alternatively, reciprocal negative feedback can permit coexistence in systems that would otherwise collapse to the competitive dominant (Bever, 2003). We hypothesized that more positive feedbacks, relative to other species, may help *So. canadensis* dominate these communities. To test these hypotheses, we used a comprehensive combination of soil community cultivation, genetic tools, and a multifactorial greenhouse experiment.

3.2 MATERIALS AND METHODS

3.2.1 Overview

We conducted these experiments at the Pymatuning Laboratory of Ecology (PLE) in

northwestern Pennsylvania (Pittsburgh, PA). We used four native old-field herbaceous species: *Solidago canadensis, So. rugosa, Symphyotrichum novae-angliae,* and *Sy. pilosum*. The *So. canadensis*/*altissima* species complex dominates old-field communities for three or more decades after agricultural abandonment throughout large portions of the northeastern and mid-western United States and southern Canada (Bazzaz, 1996; Carson & Root, 2000; Banta *et al.*, 2008). The other three focal species (*So. rugosa, Sy. novae-angliae,* and *Sy. pilosum*) are subordinates that commonly co-occur with *So. canadensis* (Banta *et al.*, 2008). We used concurrent greenhouse studies to assess whether cultured soil communities of these plant species alter plant performance and competitive ability. To support the prediction that disparate soil communities can drive plant-soil feedbacks, we subsequently used molecular approaches to quantify differences in the cultured soil communities.

3.2.2 Soil Community Cultures

Creating species-specific soil communities in the greenhouse. We cultured soil communities by growing our species from multiple, local seed sources in local field soil for 12 months in the greenhouse (following Bever 1994). We used aseptic technique throughout the soil and seed preparation. We surface sterilized seeds in a 5% bleach solution and then germinated these seeds in Conviron™ growth chambers in June 2004. Seedlings were transplanted into greenhouse trays filled with autoclaved silica sand and fertilized with a ½ strength Hoagland's solution twice weekly. Single seedlings (with at least 2 true leaves) were then transplanted into pots (20 cm X 15 cm) filled with a 3:1 ratio of topsoil (collected from an early successional old-field near PLE) and autoclaved silica sand. This topsoil was thoroughly chopped and homogenized before use. We used 7 replicates for each of our four species, for a

total of 28 pots. In the greenhouse, pots were randomly repositioned monthly and watered regularly without fertilizer. We harvested above ground biomass following flowering in October 2004, after 4 months of growth. These individuals subsequently resprouted and flowered, and in late June 2005 we discarded aboveground and large rhizome biomass and separated soil by species. This resulting substrate is now a soil community trained by that particular plant species (e.g. Bever 1994, Hausmann & Hawkes 2009).

Creating species-specific soil communities in the field. Soil cultures from greenhouse studies may lack critical biotic components found only in soils grown *in situ* (Sykorova *et al.*, 2007). To address this issue, we obtained soil from 5-year old monocultures of our focal species grown in the field. We established monocultures in 2000 by planting six seedlings (from ≥3 local source populations) on freshly tilled Holly silt loam soils in the center of 4 x 4 m plots in a formerly agricultural old-field near PLE (Natural Resources Convservation Service). Each of the four plant species was randomly allocated to 5 plots for a total of twenty monocultures. Each species was allowed to clonally spread and plots were weeded to eliminate heterospecifics. On July 1, 2005, we took five to seven, 2.5 cm x 20 cm soil cores from within the monoculture of each plot. These soil samples were combined and sealed in polyethylene bags and immediately stored at 4˚C until inoculum preparation. In the summer of 2008, three additional soil samples were taken from each monoculture; these samples were sent to the Agricultural Analytical Services Lab at Pennsylvania State University for soil chemistry analyses.

Preparation of inoculum pooled from field and greenhouse soil. We pooled soil from our greenhouse and monoculture experiments to create inoculum to test whether differences in soil communities could alter the performance of our focal plant species. Soil from the

greenhouse and monocultures, including root fragments, was thoroughly chopped and homogenized in a 1:1 ratio. The soil was divided equally into two portions: one immediately stored at 4˚C to use as 'live' soil inoculum, and one autoclaved to use as sterile inoculum. To minimize abiotic effects, each 'live' soil inoculum was composed of equal parts of each soil community, with all but one autoclaved (Bever 1994). For example, *Solidago canadensis* inoculum was composed of live *So. canadensis* soil and autoclaved *So. rugosa, Symphyotrichum novae-angliae,* and *Sy. pilosum* soil communities, in a 1:1:1:1 ratio. A sterile control was composed of autoclaved soil communities of all 4 four species. Additionally, we immediately stored 250 grams of all live soil communities in -80˚C freezer for subsequent genetic analyses.

3.2.3 Do soil communities alter metrics of plant performance?

We used a factorial design in the greenhouse to test if different soil communities alter the performance of *Solidago canadensis, So. rugosa, Symphyotrichum novae-angliae,* and *Sy. pilosum.* We filled 30 cm diameter pots with a mixture of 2 kg of autoclaved local field topsoil and silica sand (3:1 ratio). We randomly assigned soil community and sterile control to pots. We mixed 128 grams of pooled soil inoculum into the top 5 cm of soil using 1:16 ratio of soil community inoculum to sterile field soil. This multiple species mixture, sterilization, and dilution methodology (see Preparation of inoculum above) minimizes abiotic effects and thus the impacts on plant performance are most likely due to differences in soil community. Over six days in early July 2005, we planted 4 sterile-reared seedlings (as described above) of a plant species in each pot. Our design consisted of 4 species grown factorially in 5 soil communities (*So. canadensis, So. rugosa, Sy. novae-angliae, Sy. pilosum,* or sterile control), replicated 7 times for 140 pots. Pots were placed in a greenhouse at PLE without supplemental lighting, re-

randomized every 2 weeks and watered to saturation 2-3 times weekly. After four months, following flowering, aboveground biomass of all pots was harvested and dried at 60˚C to constant mass and weighed.

Statistical analysis of soil community feedback. We tested the effects of plant species, soil community origin, and their interaction on per capita aboveground biomass using analyses of covariance in PROC MIXED of SAS version 9.2 (SAS Institute 2009), with planting date as a random covariate. Separate ANOVAs were subsequently performed for each plant species with Tukey's corrected least squared multiple comparison tests. Additionally, because we wanted to examine differences between the dominant versus subordinate species response to home and away soil communities, we contrasted all subordinate species biomass (*So. rugosa, Sy. novae-angliae,* and *Sy. pilosum*) together against the dominant species (*So. canadensis*) grown in home and *So. canadensis* soil and the biomass of *So. canadensis* in home and all subordinate soils.

We tested for positive or negative feedback with "home vs. away" contrast statements for paired plant species (Turkington & Harper, 1979; Bever, 1994) using the general linear models procedure in SAS. Soil community feedback (interaction coefficient, Is, sensu Bever *et al.*, 1997) contrasts are calculated as

$$I_s = A_a - A_b + B_b - B_a \quad (1)$$

where A_α is biomass of plant A in plant A soil, A_β is biomass of plant A in plant B soil, B_β is plant B biomass in plant B soil, and B_α is plant B biomass in plant A soil. Values can run from positive to negative and identify the direction and magnitude of feedback. Negative feedback can arise by one or both species performing better in its competitor soil. Positive feedback is the reverse, occurring when relative performance is greater in home soil. Strong

positive feedback predicts competitive exclusion while negative feedback can result in cyclically fluctuating plant performance than can maintain diversity (Bever *et al.*, 1997; Bever, 2003). This metric is especially useful as it makes community-level predictions for the two compared species. For example, if all species responded similarly to a soil origin, feedback values (*sensu* Bever 1997) would be near zero and therefore indicate no net feedback, while other metrics may show definitive species-level feedback.

3.2.4 Do soil communities change the nature of interspecific competition?

We tested whether soil communities can differentially alter the strength of interspecific competition. *Solidago canadensis, So. rugosa, Symphyotrichum novae-angliae,* and *Sy. pilosum* were grown in pairwise competition in their own, their competitor's, and sterilized soil communities. Our methodology is identical to the intraspecific experiment described above, except two sterile-reared seedlings of each of two plant species were planted into each pot, with plant species alternated. In all, our design consisted of 6 pair-wise plant competition combinations, 3 soil communities (home, competitor, sterile) and 7 replicates for 126 pots. This experiment was conducted simultaneously with the intraspecific feedback experiment described above.

Data and statistical analysis of feedback on competition. We evaluated whether plant-soil feedbacks altered the nature of intra- vs. interspecific competition by using a Relative Interaction Intensity index (RII) :

$$RII = \frac{P_C - P_M}{\max |P_M| \text{ or } |P_C|} \quad (2)$$

where P_C is the per capita biomass of the focal plant species in *inter*specific competition and P_M is the per capita biomass of the focal plant species in *intra*specific competition or monoculture (Howard & Goldberg, 2001). The denominator is whichever value (intra- or interspecific per capita biomass) is larger. The RII metric is confined to the range -1 to +1 and scales symmetrically around zero. Positive values indicate that the strength of interspecific competition is greater than intraspecific competition. Negative values indicate the reverse, i.e., plant growth is more limited by conspecifics, indicative of overyielding. We calculated RII for each focal plant species with each plant competitor in home, away and sterile soil communities.

We tested the effects of focal plant species, plant competitor species, soil community origin, and all interactions on Relative Interaction Intensity in PROC MIXED of SAS (SAS Institute 2009), with planting date as a random covariate. Separate ANOVAs were performed at the focal plant species and focal x competitor interaction levels with Tukey's corrected least squared multiple comparison tests. We analyzed feedback identically as the monoculture experiment with a factorial ANCOVA and subsequent contrast statements in SAS.

3.2.5 Do soil community feedbacks alter plant population projections?

Our data allows us to partially parameterize the soil community feedback model first proposed by Bever (2003) to evaluate if experimentally-derived feedback values alter classical competition predictions. The soil community feedback model modifies the Lotka-Volterra competition model as

$$\frac{dN_A}{dt} = r_A N_A \left(1 + a_A S_A + b_A S_B - \frac{N_A + c_B N_B}{K_A}\right) \quad (3)$$

where N_A is the biomass (or density) of plant A*;* r_A the population growth rate of plant A*;* α_A, the change in growth rate of plant A in home soil; β_A the change in growth of plant A in competitor soil; c_B, the relative competitive effect of plant *B* on plant A; K_A, the carrying capacity for plant A in the absence of feedbacks and competition; and S_A and S_B are the relative abundances of plant A's and B's soil community, respectively. Similarly, soil community dynamics (relative change in soil community) are described by:

$$\frac{dS_A}{dt} = S_A(1 - S_A)\left(\frac{N_A}{N_A + N_B} - \nu\frac{N_B}{N_A + N_B}\right) \quad (4)$$

where ν is the relative influence of plant B on the soil community. We parameterized these models with data derived from both monoculture and interspecific competition experiments. Competition coefficients were calculated as the difference between intra- and interspecific competition biomass in sterile conditions. Feedbacks were determined from relative comparisons of biomass between sterile and specific soil communities. To isolate competition-feedback dynamics and avoid unknown parameters, all species were given identical population growth rates, carrying capacities, and initial population sizes (see Figure. 3.4 for parameters). To test the influence of plant-soil feedbacks, we ran models with and without feedback parameters, whereby Bever's feedback model (Equation 3) collapses to the classic population Lotka-Volterra model (Bever, 2003).

3.2.6 Quantifying contrasting soil inoculum cultured by our focal species.

We identified differences in the bacterial and arbuscular mycorrhizal fungal communities of our original plant species inoculum by employing terminal restriction fragment length polymorphism (TRFLP) analysis (Helgason *et al.*, 1999; Vandenkoornhuyse *et al.*, 2003; Burke,

2008). We extracted DNA from four 0.5 g samples of homogenized soil inoculum from each plant species (mixed field and greenhouse trained soil) using a MO BIO Powersoil DNA Isolation kit (Carlsbad, CA). To describe the arbuscular mycorrhizal fungal community, a ~500 bp fragment of the small subunit rRNA sequence was amplified by PCR using primers NS31 and AM1 (Simon *et al.*, 1992; Opik *et al.*, 2006) following general procedures in Helgason et al. (1999). The NS31 primer was labeled with 4, 7, 2‘, 4’, 5’, 7’ -hexachloro-6-carboxyfluorescein (HEX) and the AM1 primer was labeled with fluorochromes 6-carboxyfluorescein (6FAM). PCR products were cut using *Hinf* I and *Hsp* 92 (Promega, Madison, Wisconsin, USA) restriction enzymes. We note that NS31 and AM1 primers primarily amplify arbuscular mycorrhizal rRNA, but may additionally amplify other fungal taxa (Hausmann & Hawkes, 2009, See Discussion). Analyses of the bacterial communities were conducted with bacterial domain forward primer 338f and 6FAM-labeled reverse primer 926r to target the 16S rRNA gene; TRFs were generated with *Mbo* I restriction enzyme (Fermentas, Glen Burnie, Maryland). These primers were used because they amplify a wide taxonomic range of bacteria and are commonly used in studies of soil bacterial communities and our protocol followed Burke et al (2006). TRFLPs were analyzed at the Cornell Bioresource Center using an Applied BioSystems (Foster City, California, USA) 3730xl DNA Analyzer.

Statistical analysis of soil biotic communities. We generated relative TRFLP profiles for both bacterial and mycorrhizal communities, following protocols described by Vandenkoornhuyse et al. (2003). Every distinct terminal restriction fragment (TRF), identified as a peak >1% of total peak area, was treated as identification of microbial taxa (Vandenkoornhuyse *et al.*, 2003; Burke & Chan, 2010). Our community analysis was based on the presence vs. absence of TRFs. We assessed patterns of bacterial and mycorrhizal fungi

community composition with nonmetric multidimensional scaling (NMDS) ordination for soil communities cultured by each plant species (see Frank *et al.*, 2004; Burke & Chan, 2010). We tested for significant differences among these soil biotic communities with the Jaccard dissimilarity index. We used a nonparametric, permutation-based MANOVA to test for differences in taxon composition because rare species led to violations of assumptions of normality required for parametric MANOVA (Legendre & Anderson, 1999; McArdle & Anderson, 2001). Finally, we conducted Jaccard contrasts calculated percent taxon overlap to test pairwise dissimilarity between soil communities. Analyses were conducted in R (R Development Core Team 2007), using the vegan package (Oksanen *et al.*, 2007) and adonis function.

3.3 RESULTS

3.3.1 Hypothesis 1: Soil communities differentially alter plant performance

Soil origin caused significant and highly species-specific differences in plant performance (particularly for subordinate species) that depended upon the origin of the inoculum (plant species x soil origin interaction $p = 0.035$, see Figure S3.1, Table S3.1 in Supporting Information). In general, *So. canadensis* performed better in away (i.e., subordinate) soil than home soil (Figure 3.1A, Table S3.1). Conversely, the subordinate species as a group performed significantly better in their home soils than in *So. canadensis* soil (Figure 1A).

We found significant negative feedback in monoculture for two of our six species pairs (Table S3.1, Figure 3.1B). For one pair, (*So. canadensis* vs. *Sy. pilosum*) this negative feedback

occurred because each species performed better in its competitor's soil. For the other pair (*Sy. novae-angliae* vs. *Sy. pilosum) Sy. pilosum* performed significantly better in its competitor's soil, while *Sy. novae-angliae* grew similarly in both soil origins (Figure S3.1).

3.3.2 Hypothesis 2: Feedbacks and competitive relationships

Plant-soil feedbacks were stronger in interspecific competition, relative to monoculture. Indeed, soil community origin significantly altered competitive response (as defined by Relative Interaction Intensity) for all plant species and for half of our pairwise competition trials (plant species x competitor x soil origin interaction p= 0.0059; Table S3.1, Figure 3.2). In three cases, soil community identity changed the nature of competition, determining whether intraspecific competition was stronger than interspecific competition (Figure 3.2A,C,D). Furthermore, in four cases and for all species, type and intensity of competitive interactions in live soil were significantly different from sterile controls (Figure 3.2). For example, *Sy. pilosum* was more limited by conspecifics in its own soil community, but more limited by heterospecifics (*Sy. novae-angliae*) in sterile soil (Figure 3.2D). We also detected significant soil community feedbacks in 3 of 6 possible pairwise competition trials (Figure 3.3B; Table S3.1). *So. canadensis* had increased performance in both *Symphyotrichum spp.* soil, resulting in greater biomass in subordinate soil (Figure 3.3A). In contrast, subordinates responded similarly to *So. canadensis* and subordinate home soil. This pattern results in negative feedback between *So. canadensis* and both *Symphyotrichum* species (Figure 3.3).

The presence of soil community feedbacks reversed population projections for *So. canadensis* and *Sy. pilosum*. Classic Lotka-Volterra competition models predict *Sy. pilosum* to win in competition over *So. canadensis* (Figure 3.4, solid lines). However, the feedbacks

generated by these species reverse this hierarchy thereby promoting *So. canadensis'* rise to dominance while increasing coexistence time (Figure 3.4, dashed lines). It should be noted that *Sy. pilosum* had only a slightly higher competition coefficient than *So. canadensis* in sterile conditions.

3.3.3 Hypothesis 3: Plant species culture disparate soil communities

T-RFLP analysis revealed a total of 39 terminal restriction fragments (TRFs) of arbuscular mycorrhizal fungi using restriction enzyme *Hsp* 92 and the AM1 primer and 41 TRFs using *Hinf* I and the NS31 primer in the rhizosphere of the four plant species. We also found a total of 31 bacterial TRFs using restriction enzyme *Mbo* I in the rhizosphere of the four plant species. For simplicity, we present data for the arbuscular mycorrhizal fungi community using the AM1 primer; nonparametric MANOVA and ordination analyses results from the NS31 primer were qualitatively identical. Nonparametric MANOVA and ordination analyses demonstrated that each plant species cultured highly distinct soil bacterial ($F_{3,15}$ = 4.25495, $p < 0.001$) and mycorrhizal communities ($F_{3,15}$ = 4.03485, $p < 0.001$, Figure 3.5, Table S3.2). Pairwise Jaccard contrasts and nonparametric multivariate analyses confirmed that these communities were statistically distinct (Table S3.2). Of 12 pairwise comparisons, only the mycorrhizal communities of *Sy. novae-angliae* and *Sy. pilosum* were not significantly different (p=0.097). Indeed, soil origin explained over 50% of the variation in both mycorrhizal and bacteria communities (R^2 = 0.5022, 0.5154, respectively). Taxon overlap averaged 38% and 61% across plant species pairs for bacterial and fungal communities, respectively (see Table S3.2). Overall soil community T-RFLP characteristics are presented in Tables S3.3. In contrast, soil chemistry was relatively consistent across plant species.

3.4 DISCUSSION

3.4.1 Overview

Overall, we found compelling evidence for the fundamental tenets of soil community feedback theory. Soil community feedbacks were strong enough to influence plant performance in monoculture, and alter the intensity of interspecific competition and reverse population projections over time. Additionally, we draw strong inference that plants, even closely related species from the same genus and successional stage, culture disparate soil microbiotic communities that can drive feedback. We also found compelling evidence that negative feedbacks may reinforce the dominance of a competitively superior species (Klironomos, 2002) and fundamentally alter population projections. Finally, and perhaps most importantly, our results demonstrate unequivocally that feedbacks can change the nature of competitive interactions causing intraspecific interactions to be stronger than interspecific interactions (and vice versa), depending upon the origin of the soil community. Such reversals in limitation are fundamental to species coexistence theory (Chesson, 2000).

3.4.2 Soil communities differentially alter plant performance

The performance of every plant species was dependent on soil community origin (Figure 3.2A, S3.1, Table S3.1), suggesting that species-specific, plant-soil interactions are common in these plant communities. Moreover, *So. canadensis* performed relatively better when grown in the soil of competitors (Figure 3.1A) with which it commonly co-occurs, suggesting these feedbacks could facilitate invasion into competitor territory by this dominant species. We found significant negative feedback in two pairs of species in monoculture (Figure 3.1B), caused by superior growth in the competitor's soil community. Overall, our results add to a recent and growing literature verifying that soil communities commonly alter plant performance and often result in negative feedback (Bever, 1994; Casper & Castelli, 2007; Kardol *et al.*, 2007; Casper *et al.*, 2008; Kulmatiski *et al.*, 2008).

Changes in plant performance are likely an explicit response to differences between soil communities. That said, identifying the mechanism(s) of feedback using this methodology is problematic because our black box approach collapses all belowground interactions into plant performance. We simply do not know the causal or interactive agents of the soil community that influence performance and competitive relationships. However, we believe that differences in soil microbiotic communities are driving these feedback patterns. By inoculating standardized, sterile soil with relatively small amounts of soil cultured individually by all species and sterilizing all but one, our protocol minimizes the possibility of confounding soil microbial interactions with other feedback processes (e.g., resource availability, chemical profile, aggregation, see Bever, 1994; Ehrenfeld *et al.*, 2005; Kardol *et al.*, 2006; Casper & Castelli, 2007). Additionally, soil inoculum sources were remarkably similar in soil chemistry, and feedback responses inconsistent with abiotic differences. Although it is possible that autoclaved

inoculum had altered soil structure and chemical profiles to influence plant performance and biomass allocation, the 15/16 ratio of sterile bulk soil to inoculum is expected to strongly dilute these effects. Thus, the altered plant performance across observed soil origins is most likely due to differential responses to soil microbiotic communities. The negative feedbacks observed here may be linked to an accumulation of pathogenic bacteria or fungi, poor nutrient cyclers, or host-specific inefficient mutualists, such as arbuscular mycorrhizal fungi (Bever, 2002; Packer & Clay, 2004). Additionally, indirect negative feedbacks are also possible with mismatches of host-specificity and benefit with mutualists or detriment with pathogens (Bever *et al.*, 1997).

3.4.3 Extensive soil communities feedbacks are magnified under competition

Feedbacks were more common and, in general, stronger in interspecific competition than monoculture. Indeed, in a *post-hoc* test, we found relative biomass deviation between home and away soil increased over 30% in competition compared with monoculture ($F = 7.12$, $p < 0.0084$). Overall, half of all competitive interactions were significantly altered by soil community identity and three of six species pairs exhibited significant feedbacks. As in monoculture, the dominant species, *So. canadensis* performed better in the soil cultured by two of the subordinates (*Symphyotrichum spp.*), relative to home soil. Bever (2002) and van der Putten et al. (1997) have demonstrated how an accumulation of pathogens or mycorrhizal fungi can lead to negative feedback and should diminish the performance of the abundant species(;). However, negative feedbacks were never strong enough in our system to alter the competitive hierarchy between the dominant species (*So. canadensis)* and the subordinates (Figure 3.2B,C,D). Specifically, subordinates responded to *So. canadensis* competition similarly in all soil communities. Thus, subordinates may not be able to invade (or reinvade) the dominant's territory, whereas the

performance of *So. canadensis* is enhanced in the subordinate's soil. In contrast, this was not the case with another large-statured goldenrod species (*So. rugosa*) that can sometimes form dense, but small and spatially patchy, stands in old-fields. Here we found a significant positive feedback between *So. rugosa* and *Sy. pilosum* that predicts the extinction of *So. rugosa* largely because of *Sy. pilosum*'s greater performance in home soil in competition. Concordantly, *Sy. pilosum* has consistently higher population densities than *So. rugosa* in old-fields (Banta *et al.*, 2008), with feedbacks possibly providing a mechanism for *So. rugosa*'s low abundance and patchy distribution.

Overall, one unequivocal take-home message is that soil identity determined if intraspecific interactions were stronger than interspecific interactions. In fully half of comparisons, soil community identity significantly altered competitive intensity, and in three instances completely reversed the strength of intra vs. interspecific competition (Figure 3.2). For example, the strength of interspecific competition decreased drastically for both *So. rugosa* and *Sy. pilosum* in the soil community of *Sy. pilosum*, likely to result in longer coexistence (Figure 3.2B,C). While the few studies of feedback effects on competition indicate per-capita differences between monoculture and competition responses (e.g., Bever, 1994; van der Putten & Peters, 1997; ; Casper & Castelli, 2007; Kardol *et al.*, 2007; Petermann *et al.*, 2008, but see Callaway et al. 2004), to our knowledge, ours is the first to demonstrate that plant-soil feedbacks can be so strong that they determine whether competition is stronger within or between species. This is indeed a cornerstone mechanism of species coexistence: when species are more limited by themselves than by heterospecifics (Chesson, 2000). For example, the influence of plants on soil communities may create shifting, fine-scale mosaics of performance, where the strength of competitive interactions shift between intra- and interspecific. This generates spatial and

temporal heterogeneity, even within a seemingly homogeneous environment and may serve to favor one species, then another, *et cetera* over the scale of a few meters. If soil community feedbacks are strong or competitive abilities are similar or both, traditional competitive hierarchies may continuously reverse depending on neighbor and soil legacy, potentially allowing stable coexistence for numerous species (Chesson, 2000; Petermann *et al.*, 2008).

3.4.4 Congeneric species support disparate soil communities

There is growing consensus that different plant species culture disparate soil communities, from pathogens and rhizosphere bacteria to mycorrhizal fungi (Grayston *et al.*, 1998; Holah & Alexander, 1999; Vandenkoornhuyse *et al.*, 2003; Batten *et al.*, 2008). Our findings reaffirm this pattern for bacterial and mycorrhizal fungi. There are likely complex abiotic, biotic, host-specific, and trophic interactions that influence soil community constituents and diversity, and recent research indicates even genotypic differences can alter root endophytic bacterial communities in *Arabidopsis thaliana* (Bulgarelli *et al.*, 2012; Lundberg *et al.*, 2012).

Similarly, our congeneric species, even from the same community and successional stage, supported significantly different belowground communities, with only one exception (Figure 3.5, Table S3.2). Our results indicate that plants species create fine-scale community variation across very small spatial scales. Indeed, many plant communities, particularly old-fields, are characterized by distinct patches of long-lived herbaceous plants (Carson & Pickett, 1990; Bazzaz, 1996), potentially facilitating the formation of zones of distinct soil communities. This adds a definitive layer of complexity to our view of communities. Specifically, as plant species, even at the individual level, differentially deplete soil resources (Tilman & Wedin, 1991), they also culture novel and complex biotic communities belowground.

We acknowledge that the molecular methods to describe the soil microbial communities we used here are only implicative. By subsampling homogenized soil inoculum, we certainly compiled variation within plant species. Additionally, the primers we used extend an imperfect view of bacterial and mycorrhizal diversity. The "AMF" primers we used may additionally amplify a minority of other fungal taxa (Burke, 2008; Hausmann & Hawkes, 2009), and thus community dissimilarity may be due to differences in arbuscular mycorrhizal fungi, ascomycetes or a select few other fungi, or a combination of these groups. It is also very likely that the soil bacterial and fungal taxa we amplified with our primer sets and our analysis are only a subset of total microbial diversity. We simply use these fungal and bacterial TRFLPs as indicators of the larger soil community and did not attempt to link feedback to specific soil taxa. Indeed, we do not know if feedback is driven by the accumulation of specific pathogen(s) (e.g., Reinhart & Callaway, 2006) or via complex trophic interactions. However, we draw strong inference that the consistent soil community dissimilarity observed across our four plant species is indicative of plants culturing disparate microbiotic communities in the field, and these communities can drive belowground feedback.

3.4.5 Feedbacks, dominance and old-field communities

Old-field communities have seemingly conflicting characteristics: dominance by a few species in an otherwise highly diverse community over small spatial scales (Carson & Pickett, 1990; Bazzaz, 1996). *So. canadensis* may be the most abundant perennial forb in the northeastern United States and southeastern Canada (Carson & Root, 2000; Banta *et al.*, 2008 and citations therein), and its repeated pattern of dominance has defied explanation, though possibly linked to its ability to cast deep shade (Werner *et al.*, 1980; Carson & Pickett, 1990;

Carson & Root, 2000; Banta *et al.*, 2008). Here, soil community feedback may provide mechanisms that facilitate goldenrod invasion as well as potentially maintaining diversity within the system by decreasing competitive intensity. *Solidago* typically invades 2 to 5 years after agricultural abandonment (Bazzaz, 1996; Carson & Root, 2000). The relatively superior growth of *So. canadensis* in both *Symphyotrichum* soils likely hastens its invasion into early successional aster and grass dominated old-fields. The relatively poor performance of *So. canadensis* in home soil (Fig 3.2a, 3.3a, 3.4a) is predicted to decrease its competitive ability over time and thus its suppression of heterospecifics. Indeed, the replacement of *Jacobaea vulgaris* over time in European old-field is likely driven by negative feedback (van de Voorde *et al.*, 2011). However, if negative feedback decreases competitive intensity without reversing the competitive hierarchy, it may allow the persistence of competitive subordinate species (Bever, 2003) without altering the dominance of *So. canadensis*. We acknowledge that this mechanism contrasts with our prediction that *So. canadensis* should have generally positive feedbacks, but it suggests how *So. canadensis* can dominate old-fields and yet coexist with many plant species.

This study supported the predictions of soil community feedback theory (Bever, 2003), by demonstrating that species-specific soil community feedbacks reversed competitive hierarchies and increased the duration of species coexistence (Figure 3.4). This is a simplified illustration of how these species interact, but provides an empirically-generated demonstration of the potentially critical role of feedbacks in natural communities. Our plant-soil feedback population projections closely mirror natural species abundance over time (across > two dozen fields): *So. canadensis* increases in abundance to dominance over time, while *Sy. pilosum* is eventually excluded by year 30 (Banta *et al.*, 2008). In contrast, the only other plant-soil population projections found rapid plant extinction when pathogen feedbacks were considered,

helping to explain the invasion by *Ammophila arenaria* into Pacific dune communities in the United States (Eppinga *et al.*, 2006). These examples highlight the potentially dramatic role plant-soil feedbacks may play in community assembly and population dynamics. These feedbacks need not be strong to alter community dynamics – subtle changes to competitive hierarchies or access to soil resources may result in striking changes in population persistence and community structure - especially if there are minor differences in competitive ability and character displacement. Indeed, with dozens of coexisting species altering soil communities, plant-soil feedbacks may create temporal and spatial heterogeneity that fundamentally change local competitive outcomes and promote coexistence (Ricklefs, 1977; Reynolds *et al.*, 2003).

3.4.6 Conclusion

Soil community feedbacks are common, likely microbiotic in nature, and strong enough to alter performance and competition in these old-field species, and across communities and habitats. Although negative feedbacks generally promote species replacement (Kardol *et al.*, 2007), they also alter competitive interactions and facilitate invasion into competitors' territory. In our system, plant-soil feedbacks shape plant community dynamics and possibly promote coexistence, in our case, even in spite of a competitive dominant.

3.5 ACKNOWLEDGMENTS

We are grateful to James D. Bever, Scott J. Meiners, Jill T. Anderson, and Henry B.

Schumacher for discussion and statistical advice, as well as Scott A. Mangan, Wim H. van der Putten, the Charles E. Mitchell Lab, and anonymous reviewers for their insightful comments. We thank Grace S. Lloyd, Siarhei Tsymbalau, and Garland P. Waleko for their field and greenhouse assistance, and Roxanne Fisher of Chatham University for greenhouse use. This work was funded by the G. Murray McKinley Research Fund of the Pittsburgh Foundation, a NSF Doctoral Dissertation Improvement Grant (#0508012) and the Corning Institute for Education and Research. This is contribution number 281 to the Pymatuning Laboratory of Ecology.

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3.6 FIGURES

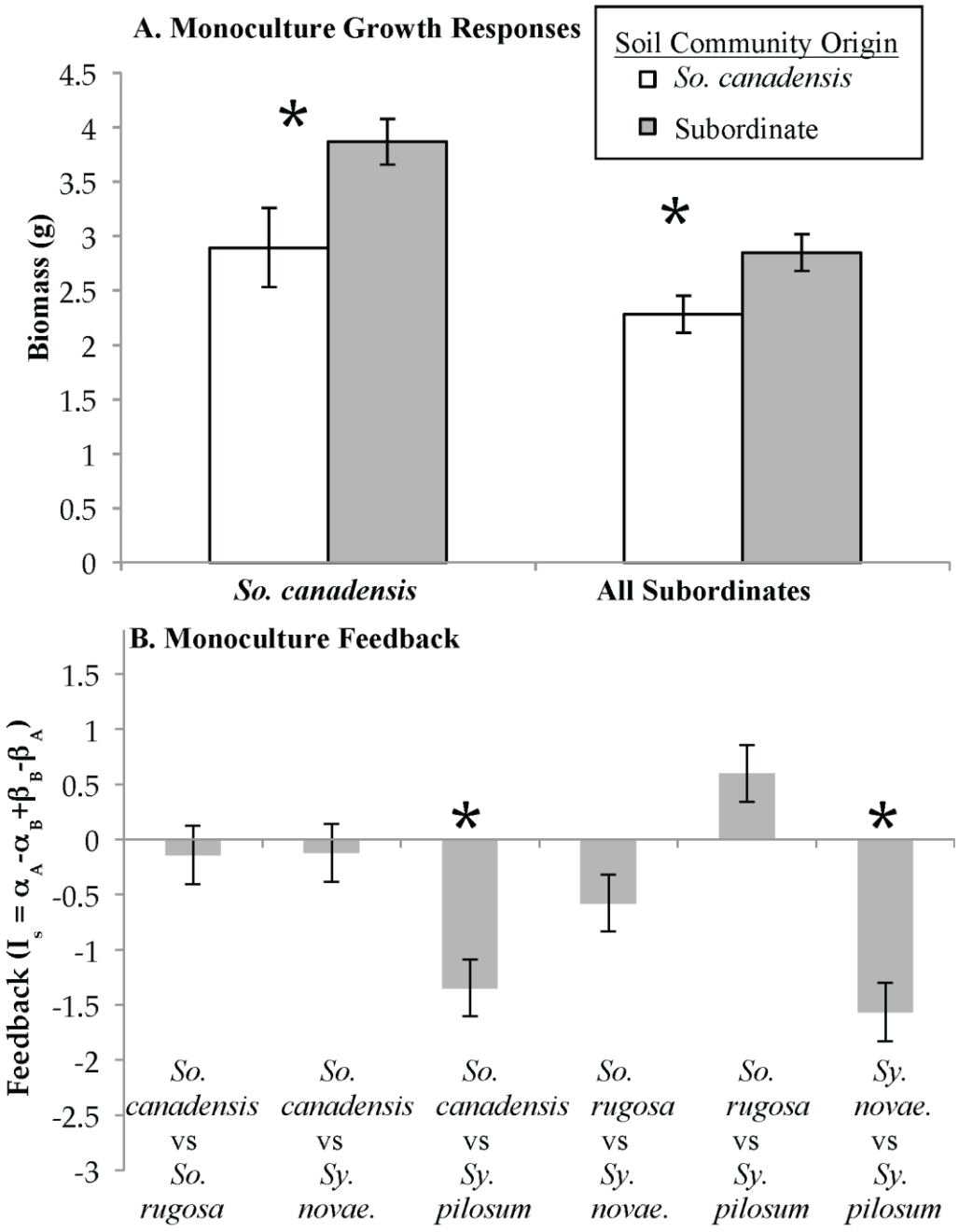

A. Monoculture Growth Responses
Soil Community Origin
So. canadensis
Subordinate
Biomass (g)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
*
*
So. canadensis
All Subordinates
B. Monoculture Feedback
Feedback ($I_s = \alpha_A - \alpha_B + \beta_B - \beta_A$)
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
*
*
So. canadensis vs So. rugosa
So. canadensis vs Sy. novae.
So. canadensis vs Sy. pilosum
So. rugosa vs Sy. novae.
So. rugosa vs Sy. pilosum
Sy. novae. vs Sy. pilosum

Figure 3.1. Monoculture growth responses and soil community feedback. Asterisks indicate significant differences or where feedback is significantly different from zero. Relevant statistics are reported in Table S3.1. **A.** Biomass of *So. canadensis* and all subordinate species in *So. canadensis* and subordinate species' soil communities. In general, all species performed better in subordinate species' soil than when grown in *So. canadensis* soil (*So. canadensis,* $p = 0.0326$; Subordinates, $p = 0.0471$). **B.** Feedback of the soil community in monoculture on the growth of four plant species. Feedback is calculated as the difference in growth of plants in their own soil community and growth in each of their competitors' soil communities (I_S, Bever 1997). *Sy. novae-angliae* is abbreviated as *Sy. novae.*

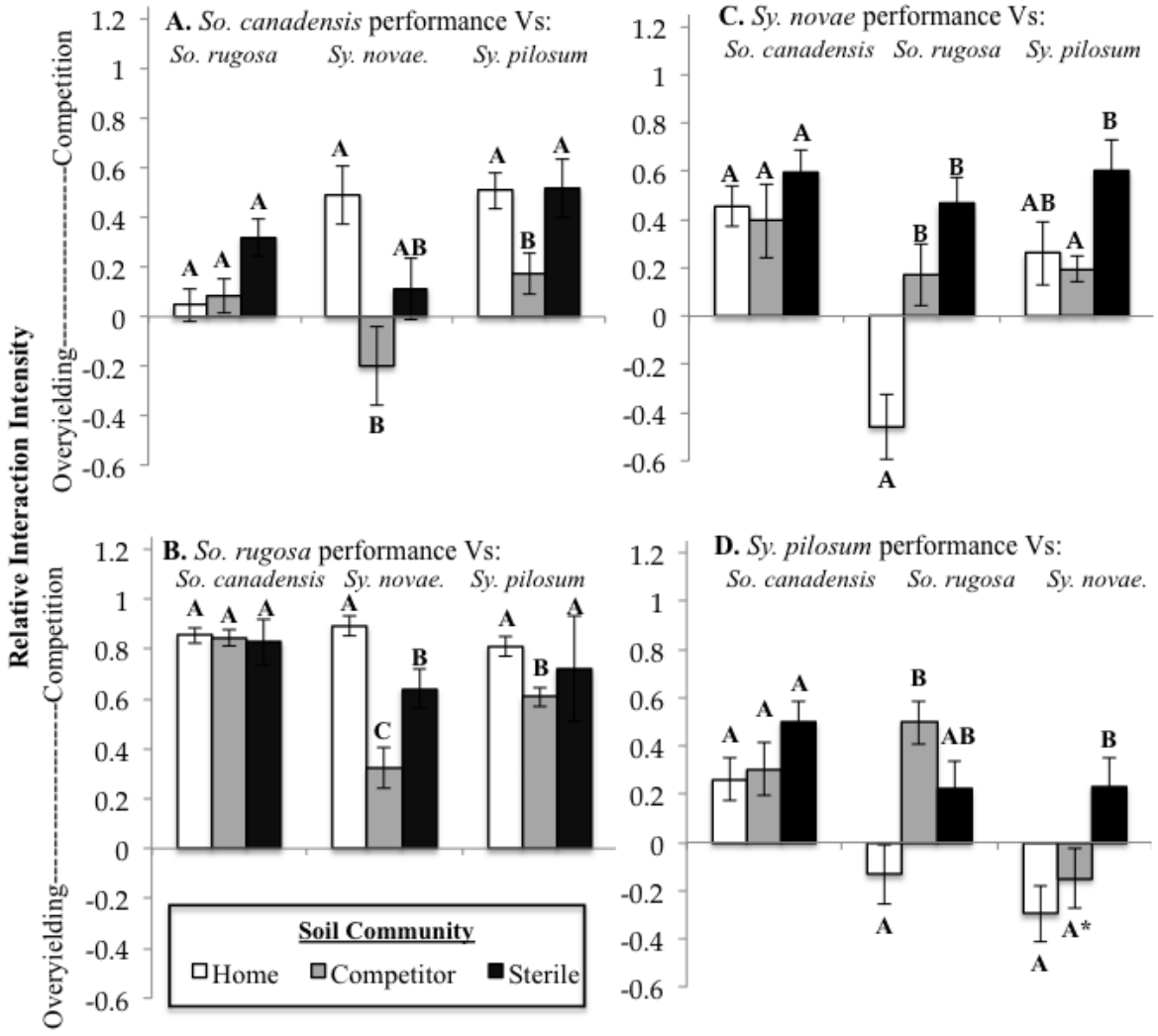

Relative Interaction Intensity
Overyielding----------Competition
A. So. canadensis performance Vs:
So. rugosa
Sy. novae.
Sy. pilosum
B. So. rugosa performance Vs:
So. canadensis
Sy. novae.
Sy. pilosum
C. Sy. novae performance Vs:
So. canadensis
So. rugosa
Sy. pilosum
D. Sy. pilosum performance Vs:
So. canadensis
So. rugosa
Sy. novae.
Soil Community
Home
Competitor
Sterile

Figure 3.2. Relative interaction intensity response of four plant species to competitors in conspecific, competitor, or sterile soil community. Competitor identity is labeled above the x-axis; the legend and shaded bars indicate soil community origin. For example, the leftmost 3 bars in Panel A displays the competitive response of *So. canadensis* to *So. rugosa* in home (*So. canadensis*), competitor (*So. rugosa*), and sterile soil communities. Capital letters indicate significant differences ($p < 0.05$) in competitive response to soil community within plant-competitor pairs. In Panel D, A* indicates a Tukey's corrected p-value of 0.067. All species had a significant response to both competitor identity and soil community origin, or a significant competitor by soil community interaction.

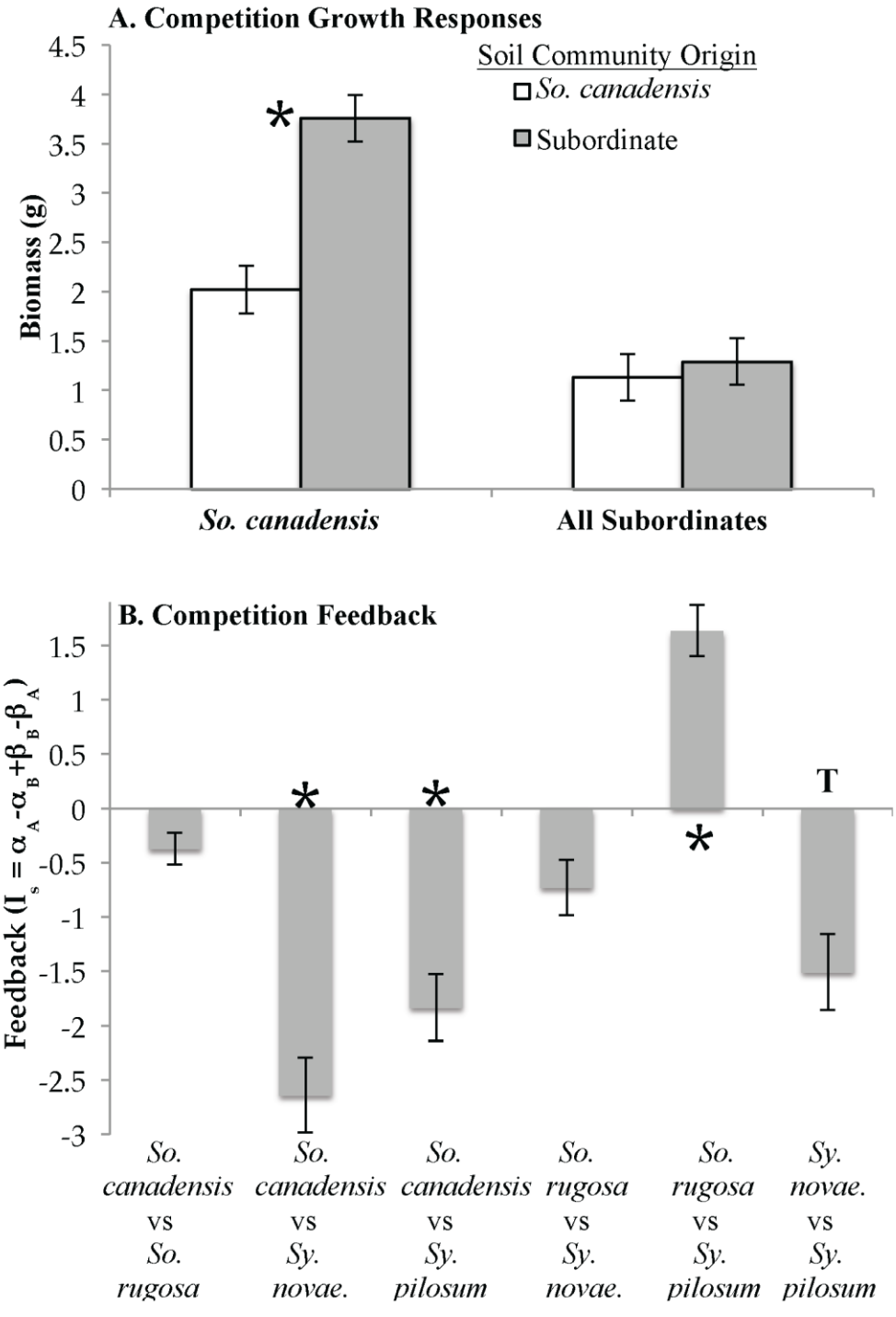

A. Competition Growth Responses
Soil Community Origin
So. canadensis
Subordinate
Biomass (g)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
*
So. canadensis
All Subordinates
B. Competition Feedback
Feedback ($I_s = \alpha_A - \alpha_B + \beta_B - \beta_A$)
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
*
*
*
T
So. canadensis vs So. rugosa
So. canadensis vs Sy. novae.
So. canadensis vs Sy. pilosum
So. rugosa vs Sy. novae.
So. rugosa vs Sy. pilosum
Sy. novae. vs Sy. pilosum

Figure 3.3. Growth responses and soil community feedback in interspecific competition. Asterisks indicate significant differences or where feedback is significantly different from zero. Relevant statistics are reported in Table S3.1. **A.** Biomass of *So. canadensis* and all subordinate species in *So. canadensis* and subordinate species' soil communities in competition. Only *So. canadensis* had increased growth in subordinate soil (*So. canadensis*, $p < 0.0001$; Subordinates, $p = 0.9637$). **B.** Soil community feedback in interspecific competition on the growth of four plant species. *Sy. novae-angliae* is abbreviated as *Sy. novae. Sy. novae-angliae* vs *Sy. pilosum* feedback displays a trend of significance with a p-value of 0.0683 (marked "**T**").

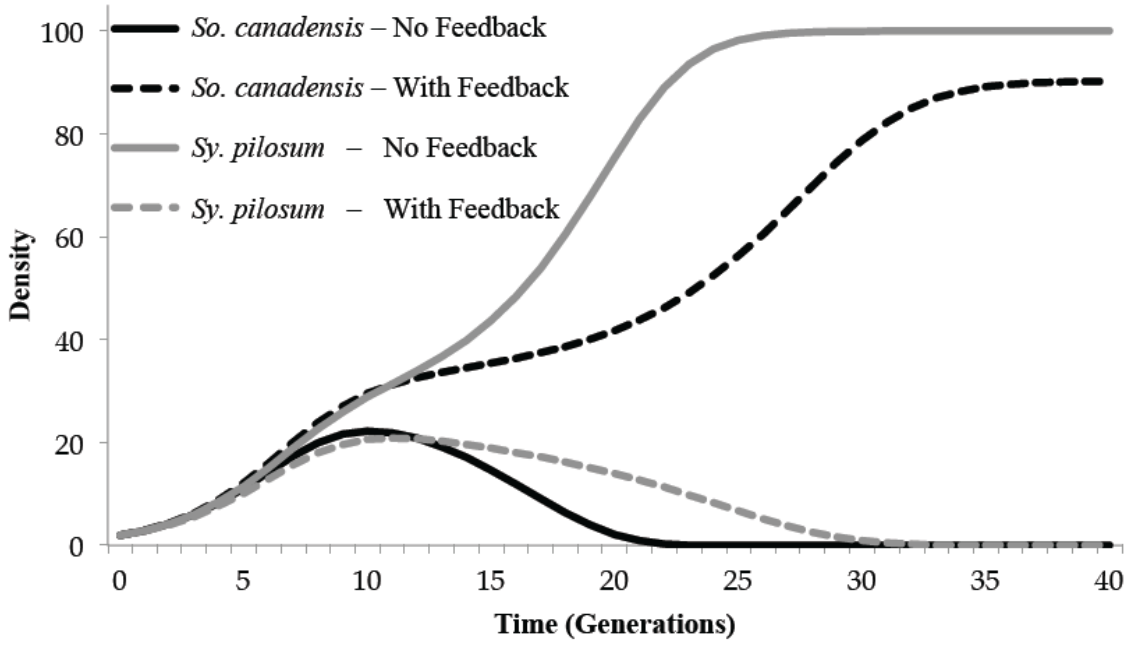
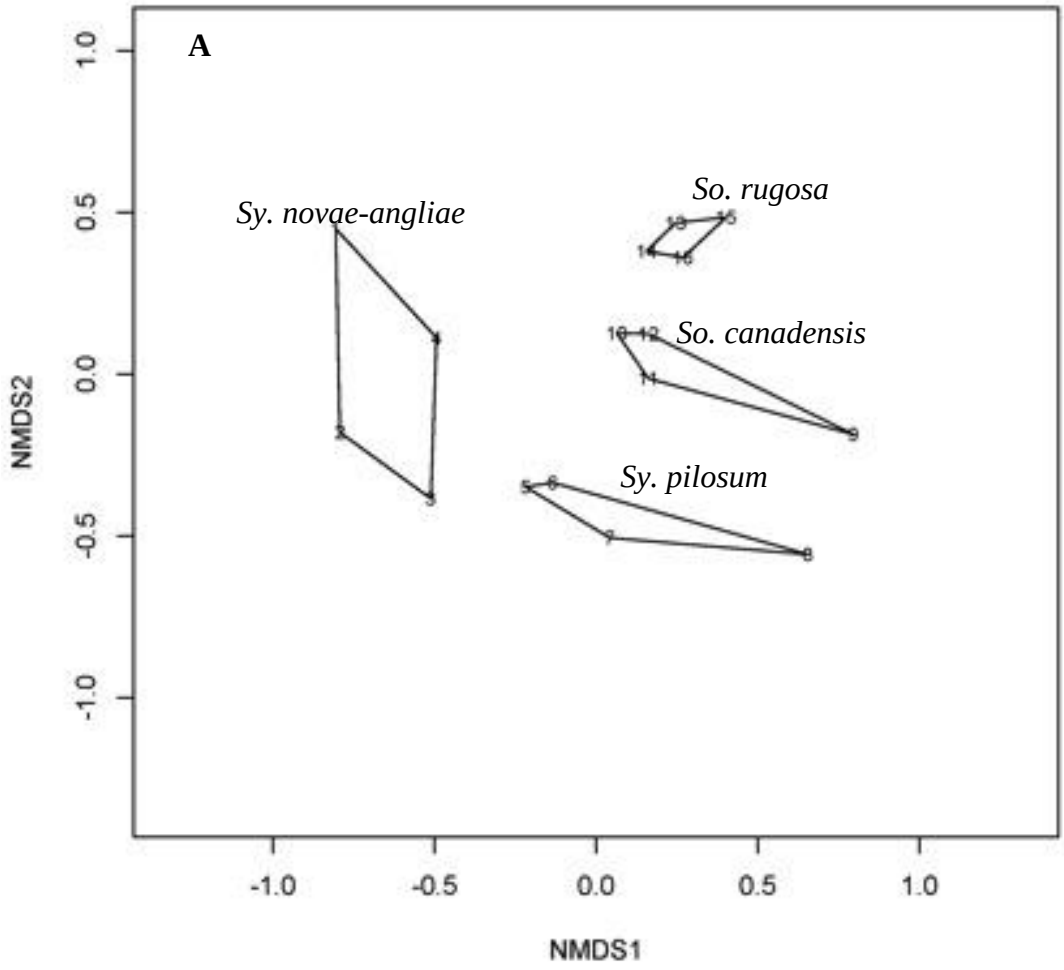


Figure 3.4. Population density projections for *So. canadensis* and *Sy. pilosum* parameterized with experimentally derived competition and soil community feedback coefficients. Projections are shown with (dashed lines) and without (solid) feedbacks. In all simulations, K =100, r = 0.5, C*SC* =2.4, and C*SP* =2.8. Species and soil communities were begun with equal frequencies. *Sy. pilosum* had a slightly greater relative impact on *So. canadensis* biomass and thus is predicted to win in competition. However, negative feedback (αSCSC =-0.097, αSCSP=-0.04, βSPSP=-0.096, βSPSC=0.192, ν=1) reverses this hierarchy and increases coexistence duration.


A
Sy. novae-angliae
So. rugosa
So. canadensis
Sy. pilosum
NMDS1
NMDS2
-1.0
-0.5
0.0
0.5
1.0

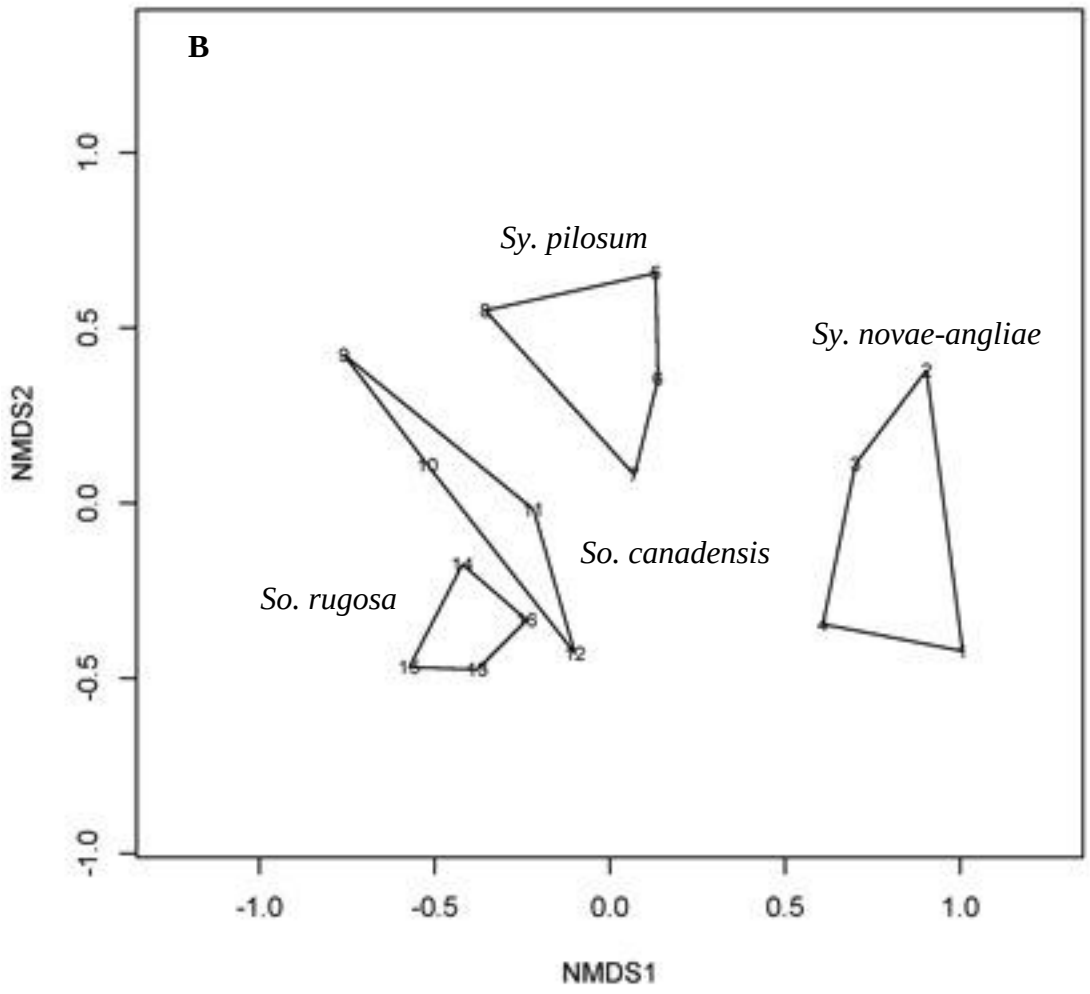

B
Sy. pilosum
Sy. novae-angliae
So. canadensis
So. rugosa
NMDS1
NMDS2
-1.0
-0.5
0.0
0.5
1.0

Figure 3.5. Nonmetric multidimensional scaling ordination of bacterial (A) and arbuscular mycorrhizal fungi (B) communities from *Solidago canadensis, So. rugosa, Symphyotrichum novae-angliae,* and *Sy. pilosum* using terminal restriction fragment length polymorphism (TRFLP) analysis**.** Each numbered data point represents a single soil sample; envelopes are drawn around replicates of soil communities of each plant species. Soil origin created consistently different belowground communities (see Table S3.2).

3.7 SUPPORTING INFORMATION

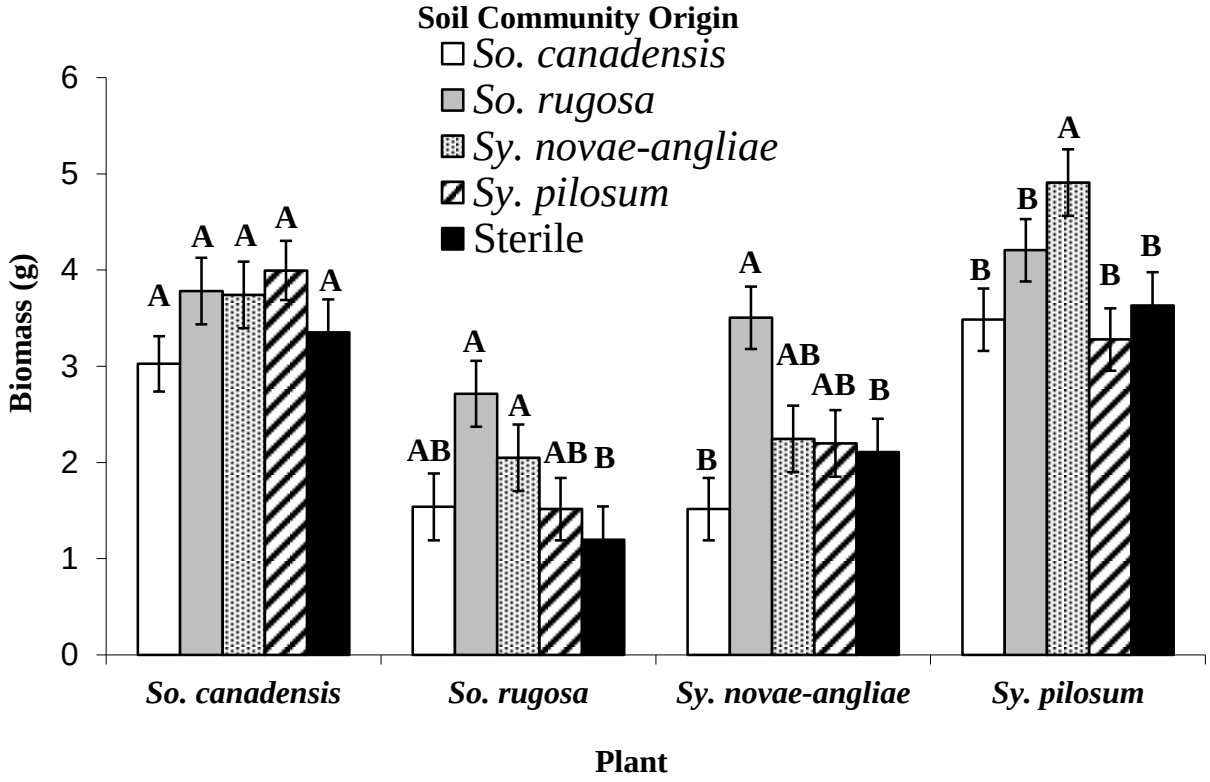


Figure S3.1. Plant growth responses of 4 old-field species in monoculture to their own, competitors', or sterilized soil communities. The legend and shaded bars indicate origin of soil community; capital letters indicate when inoculation or soil sterilization caused significant differences ($p < 0.05$) in biomass. For example, the leftmost 5 columns are the average biomasses of *So. canadensis* growing in soil inoculated with *So. canadensis*, *So. rugosa*, *Sy. novae-angliae*, *Sy. pilosum*, and sterilized soil. Error bars indicate +/- 1 standard error.

Table S3.1. Plant biomass and relative interaction intensity response to soil communities, analyzed using Proc Mixed ANCOVA. We test the generality of home vs. away soil responses, the role of dominance in soil responses, and present pairwise feedback contrasts for monoculture and interspecific competition. Boldface P-values indicate significance.

Source of Variation	F	DF (N, D)	P
Monoculture Biomass			
Plant Species	47.34	3, 119	**<0.0001**
Soil Origin	8.60	4, 119	**<0.0001**
Plant x Soil Origin	1.95	12, 119	**0.035**
General Soil Community Effects			
Away Vs Home	0.80	1, 109	0.3724
Away Vs Sterile	6.28	1, 109	**0.0137**
Home Vs Sterile	1.26	1, 53	0.2674
Dominance Effects			
Subordinate species (Home vs *So. canadensis* soil)	4.21	1, 38	**0.0471**
So. canadensis (Home vs Subordinate soils)	5.12	1, 25	**0.0326**
Relative Interaction Intensity			
Plant Species	54.41	3, 196	**<0.0001**
Competitor	14.13	3, 196	**<0.0001**
Soil Origin	2.78	4, 196	**0.0281**
Plant x Competitor	2.67	5, 196	**0.0234**
Plant x Soil Origin	4.41	12, 196	**<0.0001**
Plant x Competitor x Soil Origin	2.8	8, 196	**0.0059**
Soil Community Feedback Contrasts			
Monoculture			
So. canadensis Vs *So. rugosa*	0.01	1, 119	0.9053
So. canadensis Vs *Sy. novae.*	0.05	1, 119	0.8217
So. canadensis Vs *Sy. pilosum*	4.36	1, 119	**0.0389**
So. rugosa Vs *Sy. novae.*	0.89	1, 119	0.3462
So. rugosa Vs *Sy. pilosum*	0.86	1, 119	0.3569
Sy. novae. Vs *Sy. pilosum*	6.32	1, 119	**0.0133**
Interspecific Competition			

So. canadensis Vs *So. rugosa*	1.22	1, 24	0.2795
So. canadensis Vs *Sy. novae.*	12.16	1, 28	**0.0019**
So. canadensis Vs *Sy. pilosum*	8.12	1, 19	**0.0103**
So. rugosa Vs *Sy. novae*.	1.54	1, 22	0.228
So. rugosa Vs *Sy. pilosum*	8.26	1,28	**0.0084**
Sy. novae. Vs *Sy. pilosum*	3.64	1,28	0.0683

Table S3.2. Results of taxon overlap, nonparametric MANOVA and pairwise Jaccard Constrasts for bacterial (341 primer, MBO restriction enzyme) and mycorrhizal fungal (AM1 primer, Hsp92N restriction enzyme) communities. Results from the NS31 primer were qualitatively identical. Boldface P-values indicate significant contrasts.

	Taxon Overlap	**SS**	**MS**	**F**	**P**
MANOVA					
Soil Bacteria		1.22865	0.40955	4.25495	**<0.001**
Mycorrhizal Fungi		1.62037	0.54012	4.03485	**<0.001**
JACCARD CONTRASTS					
Soil Bacteria					
Sy.novae Vs *Sy.pilosum*	0.80	0.20728	0.20728	4.25908	**0.020**
So.canadensis Vs *Sy.novae*	0.54	0.42118	0.42118	9.42119	**0.009**
So.rugosa Vs *Sy.novae*	0.65	0.54897	0.54897	12.77897	**0.016**
So.canadensis Vs *Sy.pilosum*	0.56	0.21313	0.21313	4.74709	**0.016**
So.rugosa Vs *Sy.pilosum*	0.67	0.36740	0.36740	8.51452	**0.011**
So.canadensis Vs *So.rugosa*	0.46	0.30308	0.30308	2.86690	**0.024**
Mycorrhizal Fungi					
Sy.novae Vs *Sy.pilosum*	0.39	0.20876	0.20876	1.77810	0.097
So.canadensis Vs *Sy.novae*	0.42	0.63938	0.63938	6.88507	**0.008**
So.rugosa Vs *Sy.novae*	0.36	0.65017	0.65017	8.36860	**0.025**
So.canadensis Vs *Sy.pilosum*	0.37	0.21604	0.21604	2.77612	**0.015**
So.rugosa Vs *Sy.pilosum*	0.41	0.37358	0.37358	5.96335	**< 0.001**
So.canadensis Vs *So.rugosa*	0.33	0.18840	0.18840	3.97813	**0.024**

Table S3.3. Summary of TRFLP soil community characteristics by species and by restriction enzyme-primer combination.

Species	Taxa Richness	Richness St. Error	Total Taxa Richness	Unique Taxa	Shannon Diversity	Diversity St. Error
	Restriction Enzyme *Hsp92*, Primer AM1					
Sy. pilosum	13	1.732050808	23	7	1.994213643	0.139487795
Sy. novae-angliae	10.5	1.554563176	20	7	1.840464724	0.093799103
So. canadensis	7.5	1.322875656	14	3	1.561561938	0.091437599
So. rugosa	10.25	0.853912564	18	5	1.861733602	0.059289209
	Restriction Enzyme *Hinf 1*, Primer NS31					
Sy. pilosum	9.75	1.181453907	21	8	1.749098819	0.135396583
Sy. novae-angliae	12	1.08012345	22	8	2.023255064	0.105265302
So. canadensis	10.5	2.62995564	18	7	1.890434527	0.289410316
So. rugosa	11	0.816496581	17	7	1.981782526	0.070838803
	Restriction Enzyme *Mbo1* FAM					
Sy. pilosum	13.25	1.75	17	1	2.138219848	0.125400046
Sy. novae-angliae	14.75	0.853912564	19	1	2.288967989	0.105077578
So. canadensis	13.5	0.5	20	6	2.299742692	0.070402006
So. rugosa	13.5	0.957427108	21	5	2.16294609	0.054776796

4.0 CONDITIONALITY OF MUTUALISM: COSTS AND BENEFITS IN A TRI-TROPHIC OLD-FIELD SYSTEM

4.1 INTRODUCTION

All species exist within complex trophic webs characterized by cascading and indirect effects that potentially mediate the structure of communities and patterns of dominance (e.g., Wootton 1994). Due to the complicated nature of species interactions, it is challenging to identify the processes that structure communities and explain patterns of abundance (Vandermeer 1969, Billick and Case 1994, Abrams 1995). Indeed, some theory suggests that predictability declines with increasing diversity (Huisman and Weissing 2001) because strong indirect effects "gravely complicate the prediction of interactions in complex communities" (Morin 1999). If most combinations of interacting species in most environments are special case scenarios, then community ecology simply becomes an encyclopedia of special cases. I argue, however, that ecologists can predict community structure if the key operating mechanisms of species interactions can be identified (Relyea and Yurewicz 2002) and studies focus on critical interaction hubs.

Here, I examine two ubiquitious trophic interactions that shape terrestrial plant communities: herbivory and mycorrhizal fungi. Herbivores, and especially insect herbivores, can have strong effects on resource acquisition and thus reduce plant performance and abundance (Fretwell 1977, Huntly 1991, Brown and Gange 1992, Chase et al. 2000). Insects may function as classic keystone predators (*sensu* Paine 1966) by reducing the performance and abundance of the competitive dominant and thereby enhancing alpha diversity. Although there is strong theoretical support for this (Grover 1994, 1997, Holt et al. 1994) there still are only a fairly small number of empirical field-based examples (e.g., Brown and Gange 1992, Fraser and Grime 1998, 1999, Carson and Root 2000, Long et al. 2004). Additionally, there is now a consensus that mutualists, specifically mycorrhizae, structure terrestrial communities (van der Heijden et al. 1998b, Bever 2002b, Klironomos 2002), yet these mutualists are rarely integrated into competition and trophic web theories (but see Bever 2002a, Umbanhower and McCann 2005, Bennett et al. 2006). Arbuscular mycorrhizal fungi (or AMF) represent an ancient order of fungi that form intracellular connections with the root systems of more than 70% of all plant species (Fitter and Moyersoen 1996) and are frequently characterized as a classic symbiotic relationship (e.g., Morin 1999). Arbuscular mycorrhizal fungi increase water and nutrient transfer from the soil (Allen et al. 1981, Smith and Read 1997), potentially delivering 80% of a plant's phosphorus budget, and up to 25% of the nitrogen requirement (Marshner and Dell 1994). In turn, the cost of this mutualism is the photosynthate the plant allocates to support mycorrhizal fungi; this may be 4-20% of a plant's total carbon budget (Bago et al. 2000, Douds et al. 2000, Graham 2000). However, there has been increasing awareness that the nature of this relationship is not purely mutualistic. Indeed, these associations are species- and environment specific (van der Heijden et al. 1998a, Wilson and Hartnett 1998, Vogelsang et al. 2006), and the nature of the

relationship can span from obligately mutualistic to potentially parasitic (Johnson et al. 1997, Wilson and Hartnett 1998, Johnson et al. 2003, Klironomos 2003, Jones and Smith 2004).

A number of mesocosm and greenhouse experiments demonstrate that AMF alter plant performance and competitive interactions (Allen and Allen 1990, Hartnett et al. 1993, Moora and Zobel 1996, van der Heijden et al. 1998a, Marler et al. 1999), suggesting that AMF may have strong impacts on competitive ability and plant relative abundance in the field. These findings also demonstrate that *mycorrhizal dependency* (defined as the relative variation in plant performance in the presence versus the absence of mycorrhizal fungi, Hetrick et al. 1989, van der Heijden 2003) varies substantially among coexisting species. Thus some species benefit more from mycorrhizal association than others. In a now classic example, the experimental reduction of mycorrhizae in the Konza Prairie caused a major increase in the abundance of suppressed C3 grasses and forbs and a decline in the abundance of dominant C4 grasses (Hartnett and Wilson 1999). Conversely, other field studies have shown that mycorrhizae appear to promote coexistence and increase diversity by enhancing resource availability to subordinate species (Gange 1993, Karanika et al. 2008). A number of greenhouse studies have found similar results (Grime 1987, van der Heijden et al. 1998b, van der Heijden 2004).

What remains unknown is specifically *how* mycorrhizae alter competitive interactions. However, if mycorrhizae can directly or indirectly impact the primary mechanism of competition, AMF can likely change competitive hierarchies and patterns of relative abundance (Aerts 2003, van der Heijden 2003). It seems inherent that AMF must be altering resource acquisition and/or tolerance to low resources. These are the very mechanisms that mediate plant competition as proposed by Tilman (1982) and Goldberg (1990) among others. If mycorrhizal associations are indeed important for the competitive ability of a plant species, then

they likely modify the plant's ability to draw down resources.

While many studies have found that AMF enhance plant performance, others have found weak, non-significant, or negative effects (e.g., van der Heijden et al.1998a, Klironomos 2003). This may be because AMF are of little consequence at the community level or it may be that their impact is context dependent. For example, the benefits to plants associating with mycorrhizal fungi generally increase as soil fertility decreases (Hoeksema et al. 2010). However, mycorrhizal fungi can also mitigate herbivore stress. Under moderate fertility, AMF may only be valuable when enemies reduce plant fitness, though past studies have shown that AMF can either increase or decrease plant herbivore resistance damage (Gange and West 1994, Borowicz 1997, Gange et al. 1999, Goverde et al. 2000, Kula et al. 2005, Gange et al. 2005, Bennet et al. 2009) and herbivore tolerance (Bennet et al. 2006, Bennet & Bever 2007).

Here, I address the importance of these complex biotic interactions to understand the consistent pattern of dominance in old-fields throughout the northeastern and midwestern US and southeastern Canada. A few species of goldenrods (primarily *Solidago canadensis*) dominate old-fields across major gradients in resource availability for up to four decades (Bazzaz 1996, Carson and Root 1999). The fact that goldenrods are almost always the dominant species in old-fields in the northeast supports the hypothesis that AMF are likely beneficial to goldenrods (Bever 2003) or at least beneficial under stress (e.g., when insect herbivores cause substantial damage, Carson and Root 2000). Because goldenrods are host to so many native herbivores, I posit that AMF may buffer the impact of herbivores by increasing resource acquisition and tolerance. Generally, I predict that associations with mycorrhial fungi should be most beneficial in the presence of herbivores, and that the degree of benefit should increase with relative abundance. Furthermore, if mycorrhizal fungi and insect herbivores are drivers of community

structure in these highly competitive systems, they should likely alter hierarchies of competitive ability. Experimental evidence indicates that old-fields are light limited (Carson and Pickett 1990, Carson and Root 2000), thus, light attenuation may well be the best predictor of competitive ability (see Banta et al. 2008).

4.2 MATERIALS AND METHODS

4.2.1 Overview

I conducted this experiment near the Pymatuning Laboratory of Ecology in northwestern Pennsylvania (Meadville, PA). I used seven old-field herbaceous species that vary in their abundance from being almost always dominant to those typically rare; one naturalized grass: *Elymus repens*; and six herbaceous composites: *Euthamia gramifolia, Solidago canadensis, So. gigantea, So. rugosa, Symphyotrichum pilosum*, and *Sy. prenanthoides*. Although all of these species commonly co-occur, (Banta et al. 2008), *So. canadensis* consistently dominates these old fields, while *Sy. pilosum* and other asters are typically abundant early in succession (Carson and Root 1999, Banta et al. 2008).

4.2.2 Establishing monocultures and implementing herbivore and mycorrhizae treatments

We established monocultures in 2000 by planting six seedlings (from at multiple local

source populations) on freshly tilled soil in the center of 4 x 4 m plots in an old field near PLE. Species were randomly allocated to plots in five blocks, with two plots of each species in each block for a total of 70 monocultures. Each species was allowed to spread clonally and plots were weeded to eliminate heterospecifics and any conspecifics that colonized by seed. We installed 2m high fences around all plots, with mesh small enough to exclude rabbits and woodchucks.

Herbivore treatments. Beginning in the spring of 2001, an insect herbivore removal treatment was randomly allocated to one plot of each species in each block. We applied a broad-spectrum synthetic pyrethroid insecticide, es-Fenvalerate (Dupont, USA) every 7 to 10 days during the growing season (Carson and Root 2000, Siemann et al. 2004). This insecticide has no known phytotoxic effects on these species (Carson and Root 2000, Siemann et al. 2004), breaks down rapidly in the soil, does not affect soil microbial populations (Talekar et al. 1983), and effectively reduces insect damage (Carson and Root 2000, Siemann et al. 2004). Root (1996) and Carson & Root (2000) provide a detailed justification for using this insecticide.

Mycorrhizal fungi treatment. Using these established monocultures, I imposed a split-plot design in spring of 2007, whereas mycorrhizal colonization was reduced on one half of each plot with applications of a systemic fungicide. In preparation, I inserted galvanized flashing down the center of each plot to a depth of 35 cm (see Figure 4.1**)**. A systemic thioallphanate-methyl fungicide (Topsin M 70W: Cerexagi, Inc.) was applied to a randomly selected half of each plot as a soil drench at recommended rates, 1.25 grams of active thioallphanate- methyl per m^2 every 14 days (Wilson and Williamson 2008). Topsin^{TM} is specifically recommended for this type of use (Wilson and Williamson 2008). Although I am well aware of some limitations of a fungicide approach, a number of impressive studies have used fungicides to reduce AMF effectively (e.g., Gange and West 1994, Hartnett and Wilson 1999, Callaway et al. 2003).

Furthermore, if mycorrhizal associations convey advantage to plant performance and the pesticide reduces fungal *pathogen* load, fungicide application will *underestimate* the effects of mycorrhizal fungi (Hartnett and Wilson 2002). To test the efficacy of the fungicide, I collected 2 soil cores from each side of every monoculture in mid-June of 2008, removing and washing root fragments. Root fragments were stained using trypan blue (Phillips and Hayman 1970) and mycorrhizal colonization was determined using the gridline insection method of McGonigle et al. (1990). At each intersection, I noted the presence of arbuscular mycorrhizal hyphae, vesicles and arbuscules.

Measuring traits. In June and August of 2008, I measured plant heights of 10 haphazardly-chosen individuals on each side in each plot (Carson and Root 2000) as well as light attenuation with Li-Cor line quantum sensors (1 m x 1 cm, see Stevens and Carson 2002, Banta et al. 2008). In August of 2008, I measured the heights of the 10 tallest individuals in each plot side. I also determined total stand density, clonal spread, number of main inflorescence branches, and frequency of flowering. I note that all measurements were taken without knowledge of plot or side treatment.

4.2.3 Growth Chamber Fungicide experiment

To test the efficacy and nontarget effects of our fungicide (Topsin M 70W: Cerexagi, Inc.), I conducted a growth chamber experiment with *Solidago canadensis*. I applied Topsin M and a water control to established plants inoculated with arbuscular mycorrhizal fungi (n=8). Seeds of *So. canadensis* were sterilized in a brief 5% bleach wash, and germinated in sterile filter paper in petri dishes in a 25° C Conviron growth chamber. Seedlings with at least 1 true leaf

were transplanted into cone-tainers (1.25 centimeter^2 area) filled with 1:1 ratio of silica sand and autoclaved local topsoil. Just prior to transplanting, 2 grams of whole culture of the mycorrhizal fungi species *Glomus intraradices* (INVAM WV968) was added to all cone-tainers. Plants were allowed 3 weeks of growth before fungicide treatment were incurred. I applied Topsin M at identical rates as in our field experiment, resulting in 1.57 miligrams of active thioallphanate-methyl added to each unit every 2 weeks. These plants were grown at in a 25° C and 75% humidity within a Conviron growth chamber for 20 weeks. At harvest, I collected a small portion (<1%) of washed roots from each individual to score for mycorrhizal colonization. These samples were stored in 50% ethanol before trypan staining and AMF colonization scoring as described in the monoculture experiment (Mycorrhizal Fungi Treatment). Otherwise, all above and belowground biomass was dried at 60° C and weighed.

4.2.4 Data analysis

All analyses were conducted in SAS 9.2 (Cary, NC) using the Proc Mixed procedure, unless noted otherwise. For individual stem measures in the monoculture experiment, I initially conducted MANOVAs before performing separate ANOVAs for each response variable level. I tested if stem height, reproductive architecture, and the tallest stem height was altered by species identity, the reduction of insect herbivores, the reduction of mycorrhizal fungal colonization, and all 2 and 3 way interactions, using Treatment nested within Plot (to account for split plot design) and Block as random variables. Additionally, to test if mycorrhizal dependency is contingent on herbivore stress, I calculated multiple values of mycorrhizal dependency (the relative difference in response variable between fungicide and control treatments) within each plot, using Block as a

random variable. I examined height, reproductive frequency, and light extinction as functions of mycorrhizal dependency. Species level responses were analyzed, if significant, with Tukey's least square correction. To determine the efficiency of our fungicide treatment in the monoculture and the growth chamber, I tested if mycorrhizal colonization was dependent on fungicide treatment using analysis of variance.

4.3 RESULTS

4.3.1 Results

Reduction of mycorrhizal colonization. Periodic applications of the fungicide Topsin M decreased mycorrhizal hyphal colonization by 58% ($p<0.0001$) in *So. canadensis* in our growth chamber experiment (Figure 4.2A). Interestingly, the substantial reduction of mycorrhizal colonization had no impact on total biomass *So. canadensis* ($p = 0.4783$). In the monocultures, overall mycorrhizal hyhal colonization was similarly reduced 56% by applications of Topsin M (Figure 4.2B).

Individual plant measures. We found weak to no responses in plant height and reproductive architecture to the factorial reduction of insect herbivores and mycorrhizal fungi. Although our MANOVA indicated that species did vary in their response to mycorrhizal fungi (Table 4.1. Species x Topsin, $p =0.0414$), we found only species to be a significant predictor of average height and reproductive architecture in subsequent ANOVAs ($p < 0.0001$). I did observe trends of reproductive architecture decreasing across species with reductions of mycorrhizal

colonization (p = 0.0659) and species varying in average height in response to suppression of insect herbivores and mycorrhizae (p = 0.063). However, due to our split-plot design, we lacked the power to analyze these relationships at the species level.

Measures of Mycorrhizal Dependency. In general, we found negative mycorrhizal dependency, in the context of height, across our species in the absence of herbivores (Figure 4.3, Table 4.2). More specifically, mycorrhizal plants had lower growth rates relative to plants with suppressed mycorrhizal associations *in the absence of herbivores*. In contrast, we generally found positive mycorrhizal dependency across species when insect herbivores were present (Figure 4.3, Table 4.2). With little exception, the removal of insect herbivores reversed the nature of the mycorrhiza relationship, becoming seemingly parasitic (p = 0.0211).

In contrast, we found very species-specific mycorrhizal dependency in the context of reproduction (Figure 4.4, Table 4.2). We found no general effects of reductions of mycorrhizal fungi and insect herbivores on the frequency of flowering. Instead, we found reversals in mycorrhizal benefit in two species, *El. repens* and *So. gigantea* (Species X Asana p = 0.0251). *So. gigantea* followed a similar pattern as height, with mycorrhizal fungi increasing the frequency of flowering, but only *in the presence of herbivores* (p=0.0119). Indeed, mycorrhizal fungi suppressed flowering when herbivores were removed. In stark contrast, mycorrhizal fungi promoted flowering in *El. repens*, but only when herbivores were removed (p=0.0242).

We found no evidence that suppression of mycorrhizal colonization or insect herbivores altered the ability of plants to draw down light (Table 4.2).

4.4 DISCUSSION

4.4.1 Overview

Explanations for parasitism in mutualisms often consist of either selection towards cheating or exploitative genotypes, mix-matches in host specificity, or that conditional exploitation can be maintained by favorable cost-benefit ratios (Roughgarden 1975, Johnson et al. 1997, Bronstein 2001, Bever 2002a,b, Johnson 2003, Kiers & van der Heijden 2006). Indeed, theory predicts 'defection from mutualism' if one partner can obtain benefits from the mutualism but decrease their own investment (e.g., Prisoner's Dilemma, Doebeli & Knowlton 1998, Bronstein 2001, Sachs & Simms 2006). Alternatively, abiotic and biotic variation across spatial and temporal scales can alter classical mutualistic interactions (Bronstein 1994). For example, ant defense mutualisms in *Inga vera* can become simply commensalism across resource gradients (Kersh & Fonseca 2005). Similarly, seed predators attracted to high densities of hosts can result in substantial seed loss (Connell 1969, Janzen 1970, Long et al 2003, Carson et al. 2004). However, seed predators that are also dispersers can increase dispersal distance and even density of older host age classes (Klinger & Rjmanek 2010). These relationships are also likely to become more conditional with increased biotic complexity (Bronstein 1994).

4.4.2 Mycorrhizal Mitigation of Herbivore Stress

Here, we present evidence that symbiotic and classically mutualistic relationships can span from parasitism to truly mutualistic strictly depending on the presence of natural enemies. Almost all of our old-field species had obvious reversals in mycorrhizal dependency (based on

height), where their 'mutualists' only conferred benefit conditional on the presence of an additional trophic level. This pattern of compensatory growth following herbivory follows the *modification of tolerance hypothesis* (Bennet et al. 2006). AMF may indirectly influence plant storage or directly increase limiting resources lost to herbivores (McNaughton & Chapin 1985, Kula et al. 2005, Bennet et al. 2006). Indeed, Kula et al. (2005) and Hetrick et al. (1990) demonstrated that mycorrhizal plants enjoyed increase compensatory growth following herbivory or clipping (respectively) relative to non-mycorrhizal plants. Alternatively, increased resource availability by mycorrhizal fungi may allow plants to increase allocation to defensive structures or chemistry (Rabin and Pacovsky 1985; Gehring et al. 1997; Wurst et al. 2004, Bennet et al. 2006). This subsidized allocation to defense may then allow greater biomass compared to poorly-defended non-mycorrhizal plants(*Modification of defense hypothesis;* Bennet et al. 2006*)*. It is important to note that neither of these hypotheses specifically predicts parasitism in the absence of enemies (Bennet et al. 2006).

Widespread conditional or context dependent mutualism may help to explain patterns of weak, non-significant, or negative mycorrhizal effects on plant performance (Johnson 1997, van der Heijden et al.1998a, Klironomos 2003). Although negative effects of AMFs on plant performance can exist across different environments (Francis & Read 1995, Jones & Smith 2004), generally antagonistic mycorrhizal relationships occur at extreme fertilities (Johnson et al. 2003, Egger & Hibbett 2004, Hoeksema et al. 2010).

Here, we provide an additional explanation for patterns of seemingly unhelpful or detrimental mycorrhizas. AMF may act as a stress insurance policy, or a symbiotic plastic partner, in response to fine scale temporal and spatial variation, especially with perennial species. At moderate to high fertilities and otherwise benign conditions, mycorrhizal fungi may simply

act as carbon sinks, decreasing fitness (Johnson et al. 1997, Jones & Smith 2004). This carbon cost may represent the investment in the maintenance of mycorrhizas. However, under conditions of water, nutrient, or herbivore stress, plants can increase carbon allocation belowground – stimulating AMF hyphal growth and increasing resource exchange (Johnson et al. 2003, Johnson 2010). Thus, plants can buffer biotic and abiotic oscillations over time, potentially minimizing phenotypic and reproductive responses to stress and possibly resulting in higher survivorship under drought or herbivore outbreak conditions. The ecological cost of maintaining mycorrhizal associations may indeed exceed their benefits in certain soil fertilities, habitats and time scales, but if mycorrhizas mitigate tolerance to specific stresses, they may result in increased lifetime fitness over multiple growing seasons (Bronstein 2001). As anecdotal evidence, Hoeksema et al (2010) observed that AMF relationships were more beneficial in more realistic biotic contexts. I would like to emphasize that I am not disparaging conclusions of others who have observed parasitism with AMF – there are clearly mechanisms and potential explanations for such patterns (E.g., Johnson et al. 1997, Klironomos 2000, 2003, Jones & Smith 2004). However, I argue there may be cases where apparent parasitism in the greenhouse may function as true mutualists in the field.

4.4.3 Temporal and Spatial Variation in Keystone Predation and Mycorrhizal Dependency

Shifts in the nature of mycorrhizal relationships likely to occur over space and time. For example, mycorrhizae tend to become more beneficial as soil fertility, especially phosphorus, decreases (Hoeksema et al. 2010). However, there is considerable temporal and spatial variation in insect herbivore communities and identity (Root & Cappacino 1992). For example, more than

40 species of specialist insect herbivores cause damage to *Solidago canadensis* alone (Root & Cappiccino 1992, Bazzaz 1996). Furthermore, a portion of these herbivores can outbreak periodically, drastically increasing herbivore damage (Carson & Root 1999, 2000). Changes in herbivore communities also alters top down pressure differentially across plant species (Carson & Root 2000). However, if plant benefit from mycorrhizae changes predictably with insect herbivory, as here, we may expect consistent shifts in the nature of mycorrhizal relationships over spatial and temporal time scales. Finally, we may expect inherent variation in mycorrhizal dependency as well as the degree of benefit incurred when subjected to herbivory (e.g., Hartnett & Wilson 1999). Although we did not detect significant variation among species, we certainly see trends in disparate dependency (see *So. rugosa*, Figure 4.3) and strong species-specific responses in reproductive mycorrhizal dependency (Figure 4.4). All of these mechanisms may provide temporal and spatial shifts in plant species performance, potentially providing a mechanism for long-term coexistence in these systems.

4.4.4 No evidence of trophic interactions modifying competition

The basis of trophic modification of competitive hierarchies is that mutualists and enemies directly or indirectly aid or constrain resource acquisition structures (Tilman 1988, Holt et al. 1994, Grover 1994, 1997, Aerts 2003, van der Heijden 2003). If these trophic levels alter the ability of a plant to draw down resources, relative to another competitor, mutualists and enemies can fundamentally change competitive hierarchies and potentially community structure. We found no evidence that mycorrhizal dependent plant growth scales up to alter competitive ability. Indeed, we were unable to detect a measurable impact of mycorrhizal fungi or insect herbivores

on species ability to draw down light – the presumed mechanism of competition in this system (Bazzaz 1996, Banta 2008). It is certainly possible that mycorrhizal fungi and insect herbivory is unable to substantially alter competitive regimes, especially without an herbivore outbreak (Carson & Root 2000). Alternatively, we may expect long lag times in plant response to mycorrhizal suppression – especially in long-lived perennial plants with considerable belowground storage (Bazzaz 1996). It would be very informative to observe the development of monoculture that had AMF suppressed at their inception.

4.4.5 Trophic functions in old-fields

Goldenrods now not only dominate in old-fields and disturbed habitats in its native range; *So. canadensis* and *So. gigantea* are exotic invasive species overseas and form highly productive, low-diversity stands in Europe, Asia, and Australia where they slow down forest succession and decrease land values (Hirose 1971, Takafuji 1980, Bornkamm 1984, Guzikowa and Maycock 1986, Yoneda and Okata 1987, Ellenberg 1988, Weber 1994, 1997, Jobin et al. 1996, Ding et al. 2006**)**. One primary motivation for this study was to uncover processes that contribute to the consistent dominance of *Solidago* in its home range and overseas. Although *So. canadensis* responded to mycorrhizal suppression similarly to its other coexisting species, it instead illustrate a potentially common mechanism for mitigating the effects of herbivores. Additionally, the ability to increase mutualist reward in times of stress may be another tool, but not a smoking gun, in the apparent arsenal of *So. canadensis* (Pendergast et al., unpubl.). Finally, the almost ubiquitous positive response to AMF in the presence of herbivores may provide some insight into the coexistence of almost 100 species in a system with a clear competitive dominant (Meiners et al. 2007).

4.5 ACKNOWLEDGMENTS

We are grateful to Jim Bever, Jill Anderson, Charles Mitchell, James Cronin, and Deborah Goldberg for discussion and statistical advice. We thank Siarhei Tsymbalau, Luke Worsham, Todd Johnson, Katie Walzer, and Shane M. Hanlon for their field assistance. This work was funded by the G. Murray McKinley Research Fund of the Pittsburgh Foundation, a NSF Doctoral Dissertation Improvement Grant (#0508012) and the Corning Institute for Education and Research.

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4.6 FIGURES

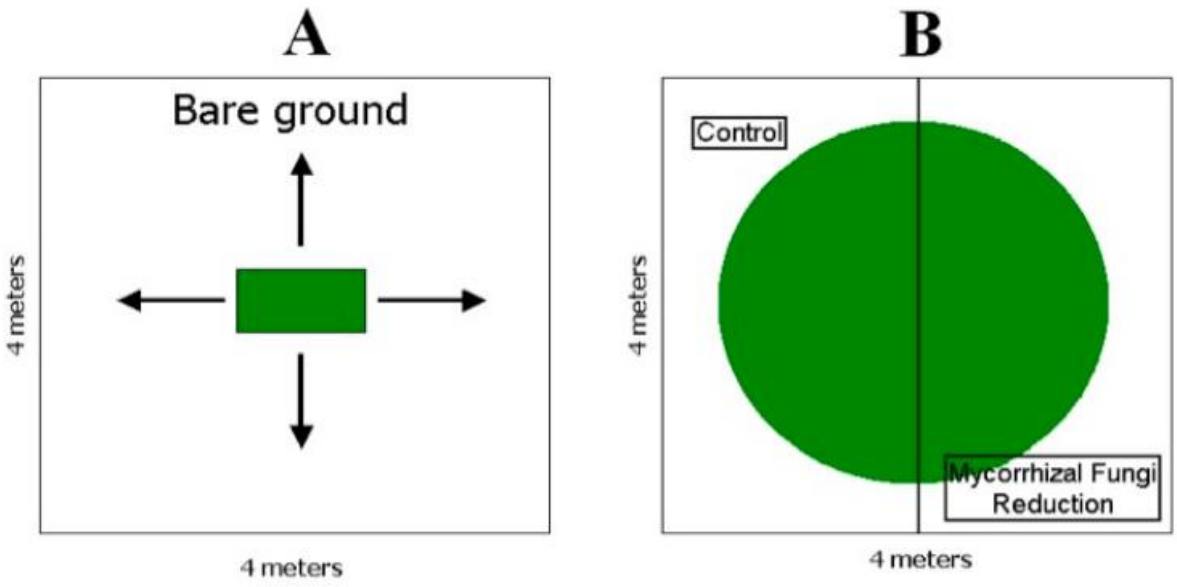

Figure 4.1. Experimental Design: A 4 x 4 m monoculture plot is on the left (A). The center-shaded area is the location where 6 initial seedlings of a focal species were transplanted in 2000. Surrounding this central area is unoccupied habitat. In 2006, the plots were bisected and galvanized aluminum flashing installed to 40 cm, and mycorrhizal fungi reduced with Topsin M® on one randomly selected side (B).

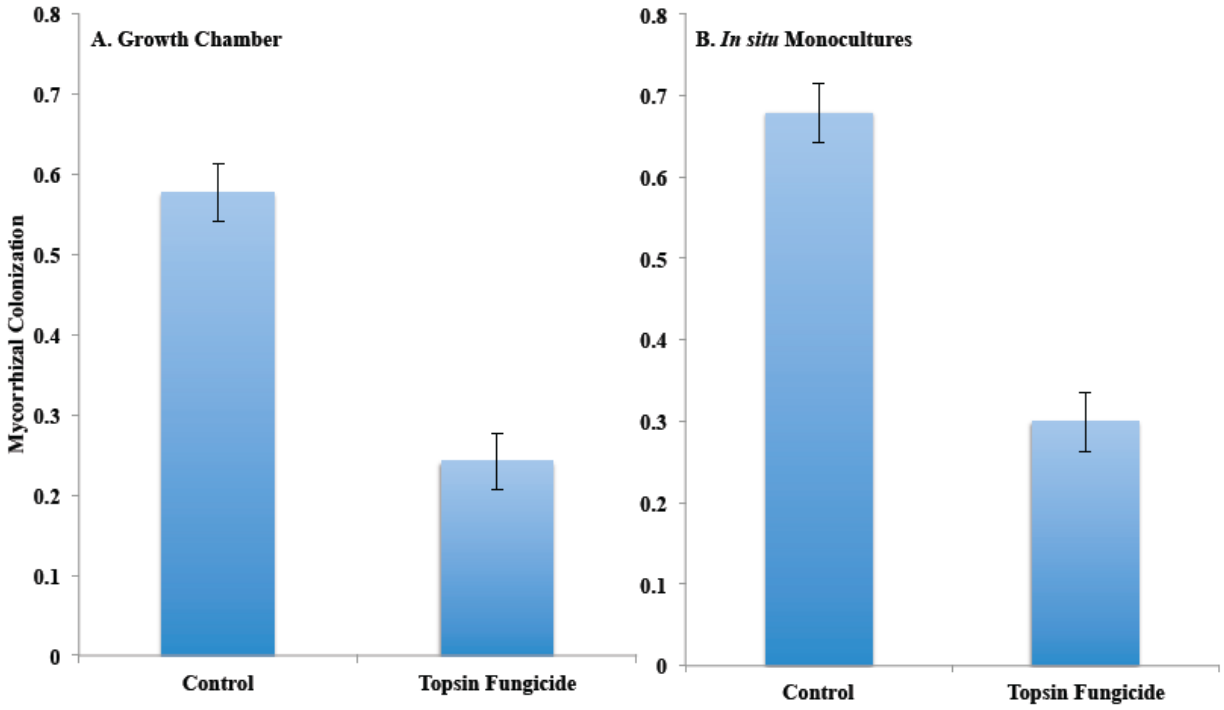

Figure 4.2. Mycorrhizal hyphal colonization in roots exposed to Topsin M fungicide and a water control in a growth chamber experiment (A) and from *in situ* monocultures. Topsin M decreased AMF colonization by 58% and 56 %, respectively ($p < 0.0001$).

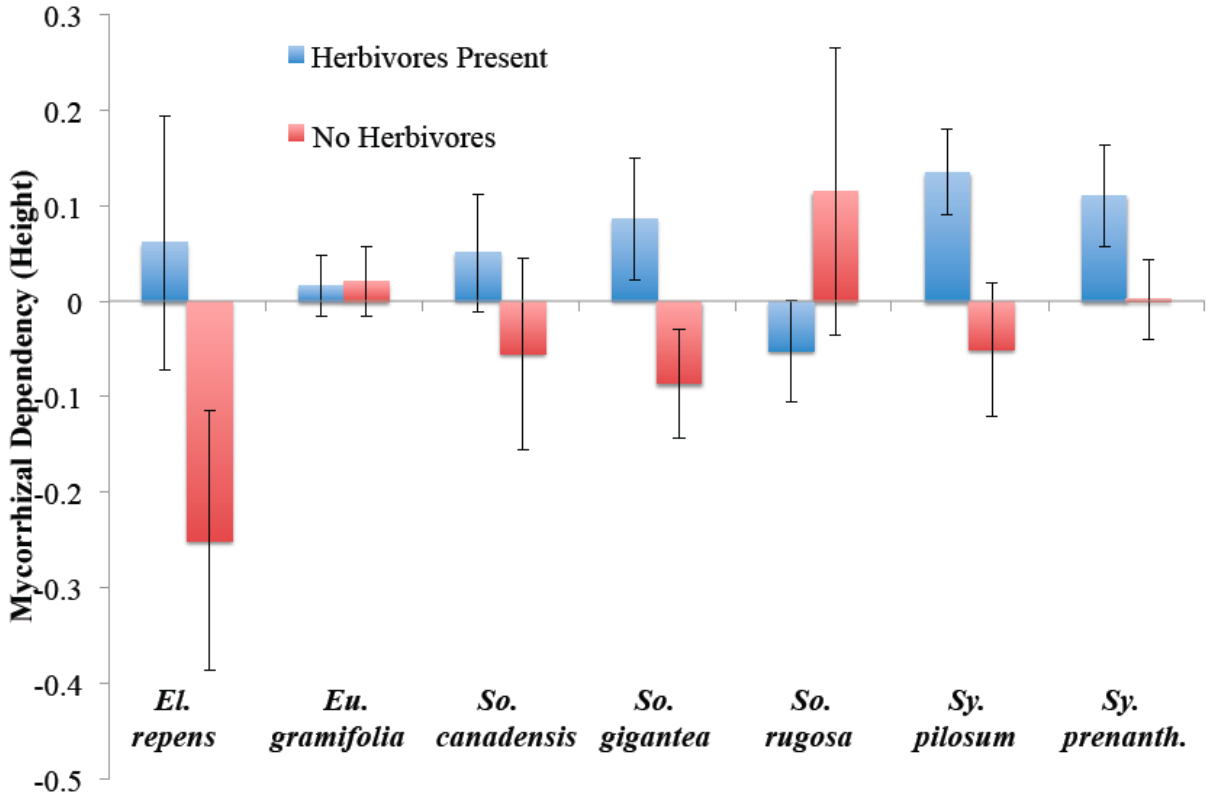

Figure 4.3. Mycorrhizal dependency based on average height. Overall, insect herbivory significantly increased mycorrhizal dependency, with compensatory growth of mycorrhizal plants relative to non-mycorrhizal plants (p=0.0211). Conversely, plant growth was generally inhibited by mycorrhizae when herbivores were absent.

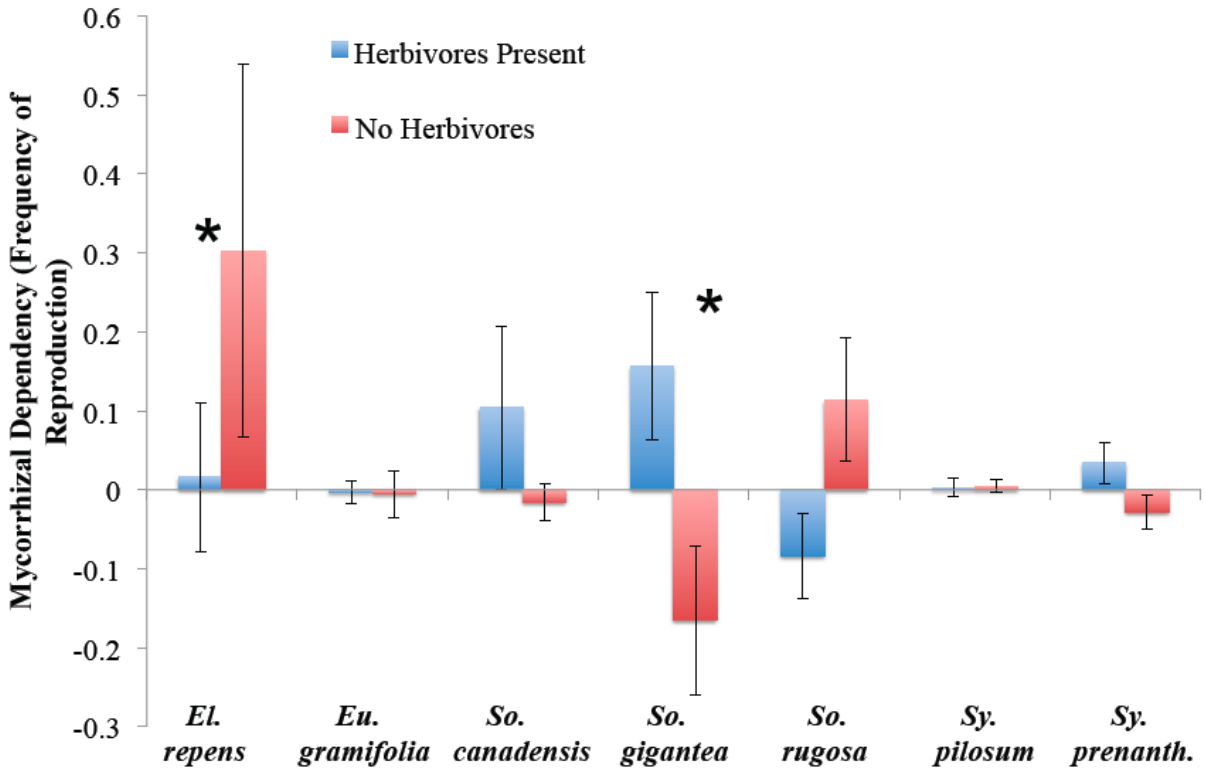

Figure 4.4. Mycorrhizal dependency based on frequency of flowering. Plant responses to AMF and insect herbivory were highly species specific with *So. gigantea* having substantially increased rate of reproduction with herbivory and mycorrhizal mutualists, relative to non-mycorrhizal conspecifics; with herbivores absent, mycorrhizae reduced flowering (p= 0.0119). Conversely, non-mycorrhizal *El. repens* had increase rates of flowering in the absence of herbivores, relative to mycorrhizal conspecifics (p=0.0242).

Table 4.1. Stem responses (average height, reproductive architechture, tallest individuals) to reductions in insect herbivory (Asana) and mycorrhizal fungi (Topsin) using Proc Mixed MANOVA and ANOVA. Boldface p-values indicate significance.

Source of Variation	Num DF	Den DF	F Value	Pr > F
Manova	1	112	716.07	<.0001
Species	6	112	18.53	<.0001
Measure*Species	6	112	18.3	<.0001
Asana	1	112	0.16	0.6929
Measure*Asana	1	112	0.12	0.7304
Species*Asana	6	112	0.53	0.7838
Measure*Species*Asana	6	112	0.89	0.5057
Topsin	1	112	1.92	0.1687
Measure*Topsin	1	112	0.03	0.87
Species*Topsin	6	112	2.27	0.0414
Measure*Species*Topsin	6	112	0.69	0.6604
Asana*Topsin	1	112	0.73	0.3944
Measure*Asana*Topsin	1	112	0	0.9473
Species*Asana*Topsin	6	112	1.03	0.4103
Measure*Species*Asana*Topsin	6	112	0.47	0.8259

Reproduction				
Species	6	969	41.71	<.0001
Asana	1	56	0.06	0.81
Species*Asana	6	969	0.13	0.9932
Topsin	1	56	3.52	0.0659
Species*Topsin	6	969	0.46	0.8379
Asana*Topsin	1	56	0.01	0.924
Species*Asana*Topsin	6	969	0.35	0.9076

Height				
Species	6	969	32.58	<.0001
Asana	1	56	0.01	0.9343
Species*Asana	6	969	1.56	0.1553
Topsin	1	56	2.5	0.1197
Species*Topsin	6	969	0.24	0.9628
Asana*Topsin	1	56	2.58	0.1138
Species*Asana*Topsin	6	969	2	0.063

Tallest				
Species	6	980	28.22	<.0001
Asana	1	56	0.9	0.348
Species*Asana	6	980	0.81	0.5594
Topsin	1	56	2.85	0.097
Species*Topsin	6	980	1.53	0.164
Asana*Topsin	1	56	0.02	0.8904
Species*Asana*Topsin	6	980	0.57	0.7506

Table 4.2. Mycorrhizal dependency (as measured as height, reproductive architecture, and light extinction) response to reductions in insect herbivory (Asana) using Proc Mixed MANOVA and ANOVA. Boldface p-values indicate significance.

Source of Variation	Num DF	Den DF	F Value	Pr > F
MANOVA				
Measure	6	28	1.55	0.1985
Species	6	357	0.84	0.5401
Measure*Species	36	357	0.75	0.8542
Asana	1	357	3.03	0.0828
Measure*Asana	6	357	0.52	0.7943
Species*Asana	6	357	3.33	**0.0034**
Measure*Species*Asana	36	357	1	0.4738
Height				
Species	6	55	0.65	0.6936
Asana	1	55	5.64	**0.0211**
Species*Asana	6	55	1.7	0.1394
Reproductive Frequency				
Species	6	55	0.91	0.4921
Asana	1	55	0	0.9498
Species*Asana	6	55	2.65	**0.0251**
Light Extinction				
Species	6	55	1.09	0.3797
Asana	1	55	0.03	0.8724
Species*Asana	6	55	1.44	0.218
Density				
Species	6	55	0.65	0.6898
Asana	1	55	0.15	0.6979
Species*Asana	6	55	0.23	0.9658